On biodiversity in grasslands:

Coexistence, invasion and multitrophic interactions

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I dedicate this thesis to my parents, the real biologists.

And to Douglas Adams (1952-2001).

CONTENTS

GENERAL INTRODUCTION

"*See first, think later, then test. But always see first. Otherwise you will only see what you were expecting. Most scientists forget that.*"
(Douglas Adams)

Biodiversity: how to coexist?

"*...., if there are really 30 or 40 million animal species, why didn't just a thousand evolve-or a billion?*" (Wilson 1985)

We know that biodiversity is currently declining at an unprecedented rate (UNEP 2008) and most people have acknowledged that we are largely responsible for this decline (Vitousek et al. 1997). Nonetheless, we have to date been unable to explain why this vast biodiversity exists in the first place. For example, "*why are there so many species of herbivorous insects in tropical rainforests?*" (Novotny et al. 2006), why 3,000 species of sea slugs in the world's oceans (Willan and Coleman 1984) or why several hundred to a thousand invertebrate species in a square meter of soil (Anderson 1975)? Many of these species are of similar appearance, have seemingly comparable life-styles and use a similar set of resources. So, how do they manage to coexist? This question lies at the very heart of Ecology and has intrigued naturalists from early on. The first studies of species coexistence attempted to assign unique jobs and living spaces even to very similar species. For example, Darwin (1859) described specific "*lines of life*" of each species and proposed that new species can evolve even in a common environment with related species. One of the first explicit references to the niche concept, which has since been widely used to explain species coexistence, is ascribed to Grinnell (1917). He wrote: "*It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships.*" An analogous concept was put forward by Charles Elton (1927). Both Grinnell and Elton viewed a species` niche mostly as its specific habitat (Schoener 1984), while Hutchinson (1957) defined the niche as an n-dimensional hypervolume and included interactions between species into his niche concept, distinguishing between fundamental and realised niches.

Today's niche models are predominantly based on resource competition with species occupying certain positions along several resource axes (e.g. MacArthur and Levins 1967) and their distance on these axes limiting the species` coexistence (the theory of limiting similarity, MacArthur and Levins 1967, Abrams 1983). One of the most cited models in this context is Tilman's R* model (1982), which predicts that species coexist if they are limited by different resources and each of them consumes most of the resource that most strongly limits its growth. After a first climax, the niche concept became unfashionable for some time, partly because of the lack of appropriate null hypotheses (Simberloff and Boecklen 1981, Lewin 1983, Chase and Leibold 2003), with some scientists even considering it "*good practice to avoid the term niche whenever possible*" (Williamson 1972). However, the concept

experienced another recent rise (Chase and Leibold 2003, Leibold 2008) after the emergence of the neutral theory (Hubbell 2001, see section "Community assembly and invasion" below).

Besides niches, other coexistence mechanisms have been proposed and tested. One example are trade-offs between species` traits that essentially equalise the inherent (i.e. density-independent) fitness of different species (Chesson 2000), preventing the emergence of a "*super-hero species*" (Rosenzweig 1995). These trade-offs can operate, for instance, between competition and colonisation abilities (Tilman 1994) or between competition and predator avoidance (Rochette and Grand 2004).

Conversely, density-dependent coexistence mechanisms do not equalise the fitness of species but rather stabilise fitness differences between species via negative feedbacks. These negative effects only set in and limit a species with higher fitness when it becomes too abundant, preventing it from outcompeting others. Effectively, classical resource niches are such a stabilising mechanism (Chesson 2000). Another example for a stabilising mechanism is the Janzen-Connell effect. This hypothesis originally intended to explain the vast species diversity of coral reefs or tropical forests (Janzen 1970, Connell 1971, Augspurger and Kelly 1984). It proposed that adult organisms (corals or trees) accumulate species-specific predators or herbivores, thus reducing the survival or vigour of conspecific offspring in their vicinity. As a result, other species are enabled to establish, promoting the coexistence of many species. In fact, a similar effect was reported for temperate forests by a French forester as early as 1905 who referred to it as the "*alternation of species*" following the death of adult trees (Schaeffer and Moreau 1958, cited in Fox 1977). However, the Janzen-Connell effect has always been somewhat elusive and its actual importance as a coexistence mechanism has not been clearly demonstrated despite the immense effort in tropical forests (Hyatt et al. 2003, Gilbert 2005).

Community assembly and invasion

"*Do natural communities assemble deterministically or does history play a strong role? …The answer…seems to be that it depends.*" (Chase and Leibold 2003)

The mechanisms promoting species coexistence in established communities are certainly closely related to the mechanisms governing initial community assembly and the invasion of new species into established communities. Again starting with Elton (1958), species invasions have been explained on the basis of vacant niches in resident communities. Similarly, Jared Diamond's (1975) "assembly rules" associate patterns of community assembly primarily with resource competition. These rules have been hotly debated, again due to the lack of testable

null hypotheses (Connor and Simberloff 1979). It was then suggested that the history of species` arrivals might be much more important than deterministic niche-based rules (Hubbell and Foster 1986, Drake 1991). This idea was supported by the fact that community assembly processes and species coexistence within established communities could in many cases be explained without the complications of niche theory or other biological processes (Connor and Simberloff 1979, Hubbell and Foster 1986, Hubbell 2001). Therefore, the neutral theory of biodiversity and biogeography (Hubbell 2001) states that under the assumption of equal per capita fitness of all species, stochasticity in species colonisation, extinction (MacArthur and Wilson 1963, 1967, Hubbell 2001) and speciation (Hubbell 2001) is the only force required to explain community assembly and species coexistence. This theory has sparked much controversy between niche and neutrality devotees but has on the positive side led to more rigorous tests of classical paradigms (e.g. Gotelli and McCabe 2002, Chase and Leibold 2003, Tilman 2004, Fukami et al. 2005, Adler et al. 2007, Cadotte 2007, Turnbull et al. 2008, Ellwood et al. 2009).

Curiously, the study of exotic invasions has been largely separate from community assembly research. The focus of this growing field has been the identification of traits imparting particular evilness to successful exotic invaders (Crawley 1986, Kolar and Lodge 2001, Sutherland 2004, Hamilton et al. 2005, Murphy et al. 2006, Richardson and Pysek 2006). Furthermore, exotic species have been hypothesised to benefit from leaving their natural enemies behind when colonising new areas (Elton 1958, Williamson 1996, Crawley 1997, Maron and Vilà 2001, Keane and Crawley 2002, Mitchell and Power 2003, Colautti et al. 2004, Agrawal et al. 2005, Joshi and Vrieling 2005, van Grunsven et al. 2007, Engelkes et al. 2008). This condition could have a general fitness-enhancing effect, essentially comparable to a trait of these species allowing them to invest more resources into their competitive ability (Evolution of Increased Competitive Ability or EICA hypothesis, Blossey and Nötzold 1995). On the other hand, the lack of enemies could merely modify the density-dependent control of invaders. The implications of the difference between these two processes have rarely been explored.

Resident communities have been shown to offer biotic resistance to invaders, consisting of competition, predation and disease (Elton 1958, Maron and Vilà 2001, Bezemer et al. 2004, Levine et al. 2004). For example, plant community diversity has been proposed to increase invasion resistance as a result of the lower availability of vacant niches for invaders (Elton 1958, Knops et al. 1999, Hector et al. 2001, Fargione et al. 2003, Turnbull et al. 2005, Mwangi et al. 2007) or as a result of the specific resistance of certain species or functional

groups (Wardle 2001, Fargione et al. 2003). Some observational studies have in contrast reported a "rich-get-richer" effect, i.e. a negative relationship between community richness and invasion resistance (e.g. Stohlgren et al. 2003). However, this negative effect of diversity was confined to large spatial scales (regions) with underlying covarying factors explaining the difference (Levine 2000).

Biodiversity and ecosystem functioning

"*…nor do we know to what degree species numbers can be raised or lowered artificially without destabilizing local ecosystems.*" (Wilson 1985)

The positive relationship between community diversity and invasion resistance illustrates the value of biodiversity for ecosystems and potentially for humans. Besides invasion resistance, a number of other ecosystem functions have been suggested to depend on diversity. The most frequently documented of these functions is certainly primary productivity (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999). In order to study the effects of terrestrial plant diversity on plant productivity, several grassland experiments were designed that manipulated the number of plant species and functional groups. Examples for these experiments are the prairie experiment at Cedar Creek in Minnesota in the US (e.g. Tilman et al. 1996), the pan-European BIODEPTH study (e.g. Hector et al. 1999), the Wageningen experiment in The Netherlands which investigates biodiversity effects in the absence of legumes (e.g. van Ruijven and Berendse 2003), another experiment in the vicinity of Wageningen which allows natural colonisation (e.g. Fukami et al. 2005, Bezemer and van der Putten 2007), the Ecotron at the NERC Center for Population Biology in London which uses climate chambers (e.g. Naeem et al. 1994) and an experiment in Zurich, that provided the soil for our first study (e.g. Wacker et al. 2008, Wacker et al. 2009). All of these studies have demonstrated that plant productivity indeed increases with plant species or functional group richness.

However, a reservation against some of these experiments has been related to the fact that low-diversity communities are proper subsets of high-diversity communities. With this design, species-rich communities may show increased ecosystem functioning simply because of an increased probability to contain a particularly productive and dominant species, i.e. a pure sampling effect instead of a "true" biodiversity effect due to niche complementarity (Wardle 2001).

The Jena Experiment in Germany, which was used for most of the studies in this thesis, was specifically designed to deal with this criticism. For example by using random species draws from a large species pool and constructing high-diversity communities consisting of

single functional groups, this experiment reduces confounding of diversity effects *per se* with effects of the presence of particular species or functional groups (Roscher et al. 2004). Affirmative of previous experiments (e.g. Tilman et al. 1996, Hector et al. 1999, van Ruijven and Berendse 2003), a positive richness-productivity relationship was found in the Jena Experiment (Roscher et al. 2005, Marquard et al. in press) and it was shown to be independent of species pool and spatial scale (Roscher et al. 2005).

Multi-trophic diversity

"*Important, but often neglected, mediators of this complexity are trophic interactions.*"
(Worm and Duffy 2003)

These biodiversity experiments have yielded a considerable amount of knowledge (reviewed e.g. by Hooper et al. 2005). However, they have been mostly confined to studying horizontal diversity effects (but see Naeem et al. 1994), i.e. the effects of diversity on ecosystem functioning at the same trophic level (the plant level). Vertical effects of species loss on functions at higher or lower levels of food webs have been largely disregarded (Duffy 2003, Balvanera et al. 2006, Duffy et al. 2007).

Albeit typically in separation from biodiversity-functioning research, the field of food web research has progressed considerably since the first descriptions of such webs (e.g. by Summerhayes and Elton 1923). These first food webs were mere reports of who eats whom, but before long, researchers acknowledged that webs should be described quantitatively (Paine 1980, Cohen et al. 1993) and the first experiments were conducted that excluded certain species in order to investigate the strength of their links with other trophic levels (Paine 1966, 1980). Today, the mathematical analysis of the structure of quantified food webs has become a complex field itself (Bersier et al. 2002, Pascual and Dunne 2006). However, experimental manipulations of habitat structure, productivity or disturbance regimes and subsequent evaluations of their effects on entire food webs, already advocated by Lawton (1984), have remained rare (Ings et al. 2009).

Since the first scientific accounts of trophic interactions, numerous hypotheses about their relative strengths have emerged and have been fervently discussed. For example, it was postulated that herbivores are not controlled by their food plants, i.e. bottom-up, but instead by their predators, i.e. top-down. This top-down control allegedly results in a "*green world*" dominated by plants (Hairston et al. 1960). Later, it was argued that herbivores might on the contrary be controlled by low plant quality (Murdoch 1966). So in the herbivores` view, the world would be predominantly prickly and tasting bad (Pimm 1991). Lawton and McNeill

finally speculated about the difficult lives of herbivores, who are "*caught between devil and the deep blue sea*" by suffering bottom-up control by plants and top-down control by predators (Lawton and McNeill 1979).

The trophic levels above herbivores could similarly be affected by bottom-up forces and, except for top-predators, by top-down forces. For example, the "nasty host hypothesis" states that the diversity of parasitoids in the tropics might be limited by the prevalence of plant allelochemicals. These plant chemicals seem to negatively affect the third trophic level via the toxicity of their hosts (Gauld et al. 1992), representing a typical bottom-up cascade (Hunter and Price 1992). The more trophic levels and species within trophic levels are involved, the more complex and less traceable these multi-trophic effects become, especially because they can be both direct and indirect (e.g. Vos et al. 2001, Tscharntke and Hawkins 2002, Dyer and Stireman 2003, Bukovinszky et al. 2008). This enormous complexity is certainly responsible for the scarcity of studies attempting to explore bottom-up cascades of species loss across more than three trophic levels, especially in natural ecosystems.

The aphid–parasitoid food web

"*Most aphids spend their lives as independent, pinhead-scale, six-legged versions of cows. They're specialized for grazing but not much else - high throughput, low drama.*" (Milius 2002)

A model system that is often used in multi-trophic studies because it is rather simple, fully quantifiable and common in many ecosystems (Müller et al. 1999), is the aphid–parasitoid food web, consisting of aphids and two to three trophic levels of parasitic wasps. Aphids are relatively specialised and immobile herbivores which typically travel longer distances only during obligatory host plant species changes as part of their life cycle (Dixon 1998). This makes them ideal study organisms to detect small-scale community changes. Furthermore, aphids are an insect group with a rather low species richness (about 4,000 species worldwide) and with fewer species in the tropics than in temperate zones. This surprising finding was attributed to the combination of specialist feeding habits, a low tolerance of food shortage and a low food plant location efficiency (Dixon et al. 1987, Dixon 1998). Still, aphids occur globally, even on sub-Antarctic islands where they have been observed to be active even in winter (Hulle et al. 2003).

In contrast, the parasitic wasps are a diverse group (about 50,000 hymenopteran parasitoids, Gaston 1991) and many have specialised to parasitize aphids. These aphid parasitoids are solitary parasitoids, laying a single egg per host. They are in turn parasitized

by solitary secondary parasitic wasps, which can even act as facultative tertiary parasitoids (Müller et al. 1999). The parasitoids` solitary mode of parasitism, along with the low mobility of aphids, allow a full quantification of trophic links (Müller et al. 1999). Because most aphid parasitoids are internal feeders (only the larvae of one group of secondary parasitoid, mummy parasitoids, feed inside the dead aphid but externally on the primary parasitoid larva), they are in close contact with the host's immune system (Askew and Shaw 1886). Therefore, they are typically much more host-specialised than predators (Memmott et al. 2000) and are expected to be strongly affected by changes in host density, species richness and quality. Indeed, lab studies have demonstrated cascading effects of low plant quality on life-history traits of secondary parasitoids (Härri et al. 2008) and the structure of aphid–parasitoid food webs has been shown to respond to changes in plant quality (Omacini et al. 2001, Bukovinszky et al. 2008). However, the consequences of declining plant species richness for aphid–parasitoid food webs and for life-history traits of the involved organisms have not been studied.

Thesis outline

The central topic of this thesis is plant diversity in grasslands. We first ask how this diversity is maintained and examine Janzen-Connell effects as potential coexistence mechanisms. We evaluate if these effects are strong enough to promote grassland plant diversity via negative soil feedbacks (Chapter 1). We then study the influence of these feedbacks on the success of exotic plant invasions (Chapter 2). We continue on the topic of invasions by investigating if community re-assembly after invasion is determined by niche-based mechanisms, such as Janzen-Connell effects or resource complementarity, or if it is driven by chance effects (Chapter 2 and 3). Finally, we assess the consequences of plant diversity loss on ecosystems: We study how invasion resistance changes with the diversity of plant communities (Chapters 2 and 3) and then proceed up the food web to examine multi-trophic effects of plant diversity (Chapters 4 and 5).

In **Chapter 1**, we explore Janzen-Connell effects, operating via negative soil feedbacks, and their influence on plant diversity in grasslands. We use soil conditioned for three years by field monocultures belonging to the Zurich biodiversity experiment. We then replant all species with and without interspecific competition on their own soils and on different soils in the greenhouse. With several soil treatments (sterilisation, activated charcoal, fertiliser and fungicide addition) we aim to identify the source of potential soil effects. A simulation model is used to determine the actual importance of these effects for the maintenance of coexistence and diversity.

In **Chapter 2**, we examine if exotic invasion success and invader dominance are more strongly influenced by the absence of negative feedbacks or by an increased fitness of invaders, for example after leaving natural enemies behind (EICA hypothesis). Furthermore, we explore the role of negative feedbacks in the biotic resistance of species-rich communities. We use both, analytical solutions and a simulation modelling approach based on feedback strengths measured in Chapter 1.

In **Chapter 3**, we investigate if invasion and subsequent community re-assembly processes are predictable according to the biology of the involved species, or if they are strongly driven by colonisation stochasticity or the community's history. We use established plant communities of the Jena Experiment varying in species richness and follow their development for three years after opening them to invasion. We furthermore compare the effects of natural dispersal and dispersal assisted by seed addition to identify the importance of stochastic colonisation.

In **Chapter 4**, we study if plant species loss exerts multi-trophic effects on the richness and density of associated aphids, their parasitoids and secondary parasitoids and if these effects are direct or mediated via lower trophic levels. We record fully quantified aphid–parasitoid food webs along a plant species richness gradient in grassland communities of the Jena Experiment. In order to distinguish between direct and indirect effects we use structural equation models.

In **Chapter 5**, we investigate multi-trophic effects of plant species loss and of related changes in aphid host plant biomass and host plant quality (in terms of nitrogen content) on life-history variables of organisms at higher food web levels. We use the same plant communities as in Chapter 4 and measure several demographic traits of aphids and parasitoids.

These chapters are followed by a general discussion, summarising findings from all studies and placing them in a larger context. Furthermore, potential applications and directions for future research are suggested.

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Fig.1: a) Field site at Reckenholz, Zurich from which soil was used for the experiment for Chapter 1, b) Greenhouse experiment for Chapter 1, c) High-diversity plant community of the Jena Experiment, d) Aerial picture of the Jena Experiment, e) Sorting of invader biomass for Chapter 3, f) Aphid counting procedure for Chapters 4 and 5, g) Aphid of the species *Uroleucon erigeronensis* (Thomas, 1878) from another experiment in Zurich (Abhilasha 2008), h) Male secondary aphid parasitoid of the species *Dendrocerus carpenteri* (Curtis) from the field site in Jena (Chapters 4 and 5).

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CHAPTER 1

Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands

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"*Pest pressure is the inevitable, ubiquitous factor in evolution which makes for an apparently pointless multiplicity of species in all areas in which it has time to operate.*"
(Gillett 1962, cited in Gilbert 2005)

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JANZEN-CONNELL EFFECTS ARE WIDESPREAD AND STRONG ENOUGH TO MAINTAIN DIVERSITY IN GRASSLANDS

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Abstract. Crop rotation schemes are believed to work by preventing specialist soil-borne pests from depressing the future yields of similar crops. In ecology, such negative plant–soil feedbacks may be viewed as a type of Janzen-Connell effect, which promotes species coexistence and diversity by preventing the same species from repeatedly occupying a particular site. In a controlled greenhouse experiment with 24 plant species and using soils from established field monocultures, we reveal community-wide soil-based Janzen-Connell effects between the three major functional groups of plants in temperate European grasslands. The effects are much stronger and more prevalent if plants are grown in interspecific competition. Using several soil treatments (gamma irradiation, activated carbon, fungicide, fertilizer) we show that the mechanism of the negative feedback is the buildup of soil pathogens which reduce the competitive ability of nearly all species when grown on soils they have formerly occupied. We further show that the magnitude of the change in competitive outcome is sufficient to stabilize observed fitness differences between functional groups in reasonably large communities. The generality and strength of this negative feedback suggests that Janzen-Connell effects have been underestimated as drivers of plant diversity in temperate ecosystems.

Key words: biodiversity; coexistence; community ecology; density dependence; functional groups; grassland; home-away effect; Janzen-Connell effect; negative soil feedback; stabilizing mechanism.

Introduction

A revolution in agriculture occurred when crop rotation was introduced to combat what became known as "soil sickness," or the faltering productivity of crops sown recurrently on the same site. For example, typical European crop rotations in the nineteenth century involved wheat, barley, turnips, and clover or peas (Overton 1996). These crops belong to what we now recognize as three different functional groups: grasses, forbs, and legumes. These plant functional groups have a taxonomic basis, and as closely related species are likely to share pests and pathogens (Gilbert and Webb 2007), the success of crop rotation schemes could be due to the avoidance of negative soil feedbacks (Bever 1994). Here, we explore negative soil feedbacks among the same three functional groups in natural grassland. If pathogens accumulate in the soil, they may reduce the chance that a related species will capture the site once a plant dies, potentially leading to natural rotations analogous to those imposed by farmers.

Studies in temperate grasslands have already shown that species can negatively affect the growth of conspecifics via the soil compartment (van der Putten et al. 1993, Bever 1994, De Deyn et al. 2003) and demonstrated a relationship between the size of such negative feedbacks and species abundances (Klironomos 2002). However, much of the work on negative soil feedbacks has focused on exotic invasions and community succession (but see Bever 1994, Olff et al. 2000, Bonanomi et al. 2005). For example, such studies have demonstrated that native–invasive interactions are strongly influenced by soil-mediated feedbacks acting via fungi or other soil organisms (Reinhart and Callaway 2006); although allelochemicals can sometimes be involved (Callaway and Aschehoug 2000). A further substantial part of the plant–soil feedback literature deals with successional dynamics, where negative soil feedbacks help to explain directed species change (van der Putten et al. 1993, van der Putten and Peters 1997, De Deyn et al. 2003).

We studied a native nonsuccessional grassland and examined how negative soil feedbacks can potentially facilitate the coexistence of species and the maintenance of diversity by acting in a similar way to the Janzen-Connell effect (Bever 2003). Janzen (1970) and Connell (1971) suggested that adults, by harboring host-specific predators and herbivores, could locally reduce the recruitment success of conspecific juveniles. However, the importance of the Janzen-Connell effect as a coexistence mechanism remains in question, because it has only been shown to operate for a single or few species within any particular community (Augspurger and Kelly 1984, Condit et al. 1992, Packer and Clay 2000, Bell et al. 2006). The prevalence and strength of the effect was therefore deemed insufficient as a

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mechanism of diversity maintenance (Gilbert 2005). The Janzen-Connell effect has also been exclusively associated with tropical ecosystems (Freckleton and Lewis 2006) or, very rarely, with temperate forests (Packer and Clay 2000, Hille Ris Lambers et al. 2002). However, negative soil feedbacks involving species-specific pathogens in grasslands can maintain diversity in a fundamentally similar way to Janzen-Connell effects: negative soil feedbacks reduce the chance of conspecific juveniles capturing sites following the death of adults, while Janzen-Connell effects reduce the chance of conspecific juveniles capturing sites close to existing adults.

We performed a controlled greenhouse experiment using common species from temperate grassland and soil collected from established field plots. We grew each species alone; but in contrast to other studies, we additionally grew each species in competition with other functional groups (Bever 2003). The influence of negative feedbacks on competitive ability has rarely been studied, potentially leading to an underestimation of their magnitude and relevance to natural communities. We concentrated on functional groups because pathogen-related effects may be more likely to maintain diversity at higher phylogenetic levels than at the species level (Gilbert and Webb 2007). In order to explore possible mechanisms behind observed effects, we applied a number of soil treatments that selectively excluded certain groups of potential feedback agents. Finally, we put our measured effect sizes into a community context by modeling how such effects interact with the inevitable fitness differences which exist between species, both within this particular community and more generally.

Materials and Methods

Soil origin and preparation

Field monocultures of 24 common European grassland species, eight grasses, eight forbs, and eight legumes (see legend of Fig. 2 and Appendix A: Table A2), were grown for three growing seasons near Zurich, Switzerland (Wacker et al. 2008). In autumn 2005, we removed four subsamples of soil per monoculture, pooled them and added 20% of washed and autoclaved sand.

We subdivided soils into a control and four treatments to investigate the general causes of potential plant–soil feedbacks. The treatments were (1) sterilization by gamma irradiation to remove all soil organisms, (2) fungicide to remove only fungi, (3) activated carbon to remove allelochemicals, and (4) fertilizer to serve as an additional control for nutrient flushes that may result from the killing of soil organisms (Troelstra et al. 2001). Fertilizer-treatment pots received a liquid NPK fertilizer once at the beginning of the experiment. There was no fertilization in any of the other treatments (see Appendix A for more details).

Experiment

The same 24 species that had conditioned the soil in the field were then grouped into eight sets, each containing one forb, one grass, and one legume species (Appendix A: Table A2). Species were reciprocally grown on their own soils ("home") and on soils from the two other species in the set ("away") in the glasshouse. We sowed seeds in monocultures on the respective home and away soils that had been subjected to the five soil treatments. There were five replicates of each combination (1800 0.2-L pots), and we recorded germination percentages after 12–20 days, depending on germination behavior of the species.

For the main experiment, seedlings were transplanted into 0.6-L pots filled with the treated soils. Communities with one of two types of competition were assembled. The first type of competition involved planting three individuals of the same species together on both the home soil and the two away soils within the set, without competition from other species (24 species $\times$ 3 soils $\times$ 5 soil treatments = 360 pots; Appendix C: Fig. C1). The second competition type involved planting one individual from each of the three species in the set together in the same pot on each of the three soils. Thus, on each soil one species was always growing "at home" while the other two were growing "away" (Appendix A: Table A2). There were three replicates per multi-species combination (8 multispecies sets $\times$ 3 soils per set $\times$ 5 soil treatments $\times$ 3 replicates = 360 pots). When the first plants started to flower after eight weeks, the experiment was stopped, all aboveground plant parts were harvested and weighed after drying at 70°C for 48 hours (see Appendix A for more details).

Data analysis

Dry mass of single plants growing on home soil was divided by the dry mass of single plants growing on away soils to get a proportional measure of feedback that is independent of plant size (in contrast to the measure used by Klironomos (2002)). For example, for species i,

$$\text{Feedback}_i = \log\left[\frac{\text{biomass}_i(\text{home})}{\text{biomass}_i(\text{away})}\right]$$

where biomass_i (home) = biomass of species i on its own soil and biomass_i (away) = biomass of species i on soil of species j (in the interspecific competition treatment, the average mass of individuals across the three replicates was used). Because each species was grown on two different away soils, each belonging to a different functional group, this resulted in two values of the feedback measure for each species per competition type and soil treatment (480 degrees of freedom in the main experiment). The ratio was log-transformed to achieve normality and homogeneity of variances. At the same time, the log transformation returns zero when there is no difference between home and away soils, and negative values for "negative feedbacks" (biomass at home smaller than biomass away) and vice versa. The log-ratio was then used as the response variable in a mixed-model ANOVA (Table A1). A similar analysis

was done with germination percentage instead of biomass for the germination experiment (Table A3).

Modeling

Our intention was to see whether a typical grass, forb, and legume could coexist given the strengths of negative soil feedbacks measured in the experiment. Thus, we modeled a simplified community consisting of three different functional groups, each containing one average or typical species. Rather than use a deterministic framework (Bever 2003), we chose a stochastic formulation to assess the impact of demographic stochasticity on persistence times. We assumed that adult individuals die at rate d and a new individual of species i is recruited to fill a site formerly occupied by an individual of type j with probability. $P_{ij} = N_i c_{ij} / \Sigma N_i c_{ij}$. Here N_i is the population size of the ith species and c_{ij} is the competitive weighting for species i at a site formerly occupied by species j. If $c_{ii} < c_{ij}$ then negative feedbacks operate, because species are less competitive when recapturing sites which they have formerly occupied.

Suitable values for the competition coefficients can be determined from our experiment, as we can assess the competitive ability of each species against identical competitors on different soil types. We can average over the eight sets to obtain robust "typical" values for each functional group. Suitable values for the death rates, d_i were estimated from field monocultures of 52 species (the entire original species pool from which our 24 species were randomly selected for this experiment). These values should typify the kind of fitness differences found between the functional groups, although some important processes are inevitably missing.

In addition to simulations including specific values estimated from the data, we also explored a range of other scenarios to examine the general relationships between fitness differences, negative feedback strengths and community size. We used four community sizes (99, 501, 999, and 5001 plant individuals) where each of the three functional groups had equal population sizes in generation 1. A proportion d_i of individuals belonging to species i was randomly selected and removed each generation during a single mortality episode (to mimic episodic mortality such as that induced by summer drought or winter cold) followed by a single episode of recruitment restoring the initial community size. We considered the persistence of the three functional groups over the long term (10 000 generations) in two ecological scenarios: (1) all functional groups had the same adult mortality rate $d_i = 0.2$ for all i and (2) there were differences in mortality rates for each functional group of either 10% ($d_1 = 0.2$, $d_2 = 0.9 \times d_1 = 0.18$, and $d_3 = 0.9 \times d_2 = 0.162$) or 20% ($d_1 = 0.2$, $d_2 = 0.8 \times d_1 = 0.16$, $d_3 = 0.8 \times d_2 = 0.128$). In each case, the probability of persistence of all three functional groups was calculated from 1000 runs each of 10 000 generations. Dispersal was global so that each functional group had the same chance of arriving at a site, although we analyzed a subset of models with local dispersal (see Appendix A).

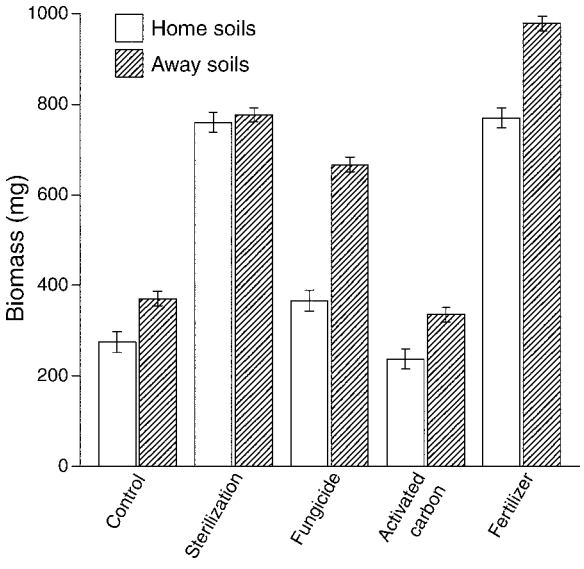

FIG. 1. Absolute biomass per plant individual (mean ± SE) on home soils (open bars) and away soils (hatched bars) for controls and the four soil treatments; data are from monocultures and three-species competition treatments combined. Only soil sterilization eliminates the disadvantage of growing on home soils.

RESULTS

We found strong negative plant–soil feedbacks throughout our study community ($F_{1,23} = 35.69$, $P < 0.001$; Appendix A: Table A1). On average, plants produced 30% less biomass when growing on home rather than on away soils (Fig. 1, "Control"), with the effect being considerably more severe when plants were grown in competition with the other two functional groups ($F_{1,23} = 16.68$, $P < 0.001$). In the pots with interspecific competition, 23 out of 24 species suffered a negative feedback (Fig. 2a, left) and plant mass was on average halved on home compared with away soils. In monocultures, fewer species experienced negative feedbacks and the effects were much weaker than in interspecific competition (Fig. 2a left vs. right). Species from each functional group grew equally well on soil from either of the other two functional groups ($F_{2,22} = 0.47$, $P = 0.634$). Furthermore, species from each functional group suffered the same magnitude of negative feedback ($F_{2,21} = 0.53$, $P = 0.595$). Within functional groups, the size of the effect varied between species ($F_{21,215} = 12.86$, $P < 0.001$). For example, the biomass reduction when growing on home vs. away soils in competition with the other two functional groups ranged from 90% in *Echinochloa crus-galli* to around 4% in *Centaurea jacea*. Only one out of 24 species, *Trifolium incarnatum*, had a higher biomass (+6%) on home soil. When grown in monoculture, the effect size ranged from

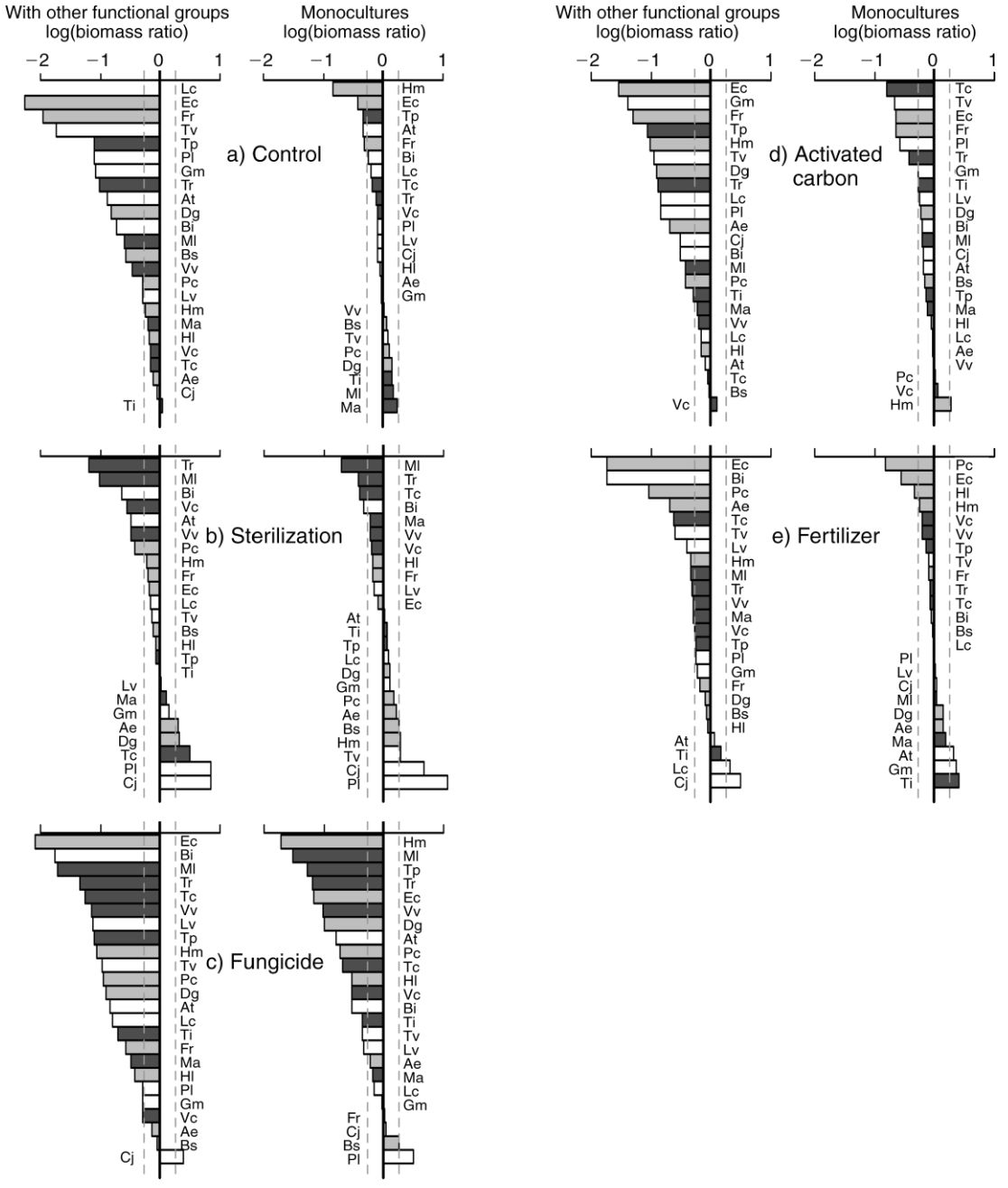

FIG. 2. Mean soil feedbacks for all 24 species of European grassland plants: biomass of individual plants on home soils was divided by biomass of individuals on away soils for each species, then log-transformed. Negative values correspond to a net disadvantage on home soils (negative feedback); positive values to a benefit on home soils (positive feedback). The left-hand column shows plants grown with competition from other functional groups; the right-hand column shows monocultures. Dashed lines show ±SE around zero. Forbs are represented by white bars, grasses by light gray bars, and legumes by dark gray bars. Abbreviations: At, *Arctium tomentosum*; Ae, *Arrhenaterum elatius*; Bi, *Berteroa incana*; Bs, *Bromus sterilis*; Cj, *Centaurea jacea*; Dg, *Dactylis glomerata*; Ec, *Echinochloa crus-galli*; Fr, *Festuca rubra*; Gm, *Galium mollugo*; Hl, *Holcus lanatus*; Hm, *Hordeum murinum*; Lc, *Lepidium campestre*; Lv, *Leucanthemum vulgare*; Ml, *Medicago lupulina*; Ma, *Melilotus albus*; Pc, *Panicum capillare*; Pl, *Plantago lanceolata*; Tv, *Tanacetum vulgare*; Tc, *Trifolium campestre*; Ti, *T. incarnatum*; Tp, *T. pratense*; Tr, *T. repens*; Vc, *Vicia cracca*; Vv, *V. villosa* (Lauber and Wagner 1996). Lc indicates the control (outlier excluded).

a 55% biomass reduction (*Hordeum murinum*) to a 25% increase (*Melilotus albus*) on home soil. In contrast to the effects on growth, there was no general home vs. away effect on seedling emergence ($F_{1,23} = 0.24$, $P = 0.627$; Appendix A: Table A3; Appendix B: Fig. B1).

Our experiment also included soil manipulation treatments designed to investigate potential mechanisms. These treatments differed significantly in their impact ($F_{4,92} = 4.68$, $P = 0.002$). Gamma irradiation removed the negative feedback almost completely (Fig. 1), particularly when species were grown in competition with the two other functional groups (Fig. 2b left). The fungicide treatment of the soil resulted in a net increase of the negative feedback compared with controls (Fig. 1, Fig. 2c left and right). The activated carbon treatment had little effect in our experiment (Fig. 1, Fig. 2d left and right), and the fertilization treatment reduced the negative feedback effect, although not as effectively as the gamma irradiation (Fig. 1, Fig. 2e left and right).

Modeling

The model parameters are particularly simple: we can use the same value of c_{ii} for each functional group as the magnitude of the negative feedbacks suffered by each functional group was the same ($F_{2,21} = 0.53$, $P = 0.595$). In addition, we can use a single value of c_{ij} for all i and j, as each functional group grew equally well when "away" on soils belonging to either of the other two functional groups ($F_{2,22} = 0.47$, $P = 0.634$). By setting the competitive weighting when capturing away sites (c_{ij}) to unity for all i and j we can vary the size of the negative feedback on home soils by choosing values for the competitive weighting when trying to capturing home sites (c_{ii}) in the range 0–1. In our experiment, species from all functional groups had roughly half the biomass when grown with the same competitors on home rather than on away soils; therefore we would estimate $c_{ii} = 0.5$ for all i. In the special case of $c_{ii} = 1$, the model becomes neutral and the only force in the community is drift. In contrast, when $c_{ii} = 0$, a species has no chance of recruiting on a home site, and the model is deterministic in the case of two species. However, there will always be stochasticity in the three-species case because species from the remaining two functional groups have an equal chance of capturing any site vacated by the third.

The model revealed that even weak negative soil feedbacks ($c_{ii} \leq 0.9$) lead to stable coexistence when different functional groups have equal fitness ($d_i = d_j$), but that stronger feedbacks are necessary to ensure coexistence when species differ in fitness ($d_i \neq d_j$, Fig. 3a). Fitness differences between species lead to unequal equilibrium population sizes and therefore increase the probability that the functional group with the lowest fitness becomes extinct. Much stronger negative feedbacks are therefore required to reduce fluctuations around the equilibrium and hence stabilize the interaction (Fig. 3a–d). The strength of negative feedback estimated here ($c_{ii} = 0.5$) would stabilize fitness differences among functional groups of around 10%, but not of 20%, even in a large community (5000 individuals; Fig. 3a). Using observed death rates of the three functional groups from field monocultures (legume $d = 0.466$, grass $d = 0.450$, forb $d = 0.364$) reveals that this value ($c_{ii} = 0.5$) is sufficient to ensure persistence of all three functional groups in communities of $\geq$500 individuals (Fig. 3, dashed lines). However, this only holds if a sufficiently high proportion of the seeds produced (more than about 50%) disperse away from the parent site (see Appendix D: Fig. D1).

Discussion

In our communities, feedback effects were strong and pervasive, and species from all three functional groups were similarly disadvantaged when competing for sites which they had formerly occupied. The effects were considerably weaker when plants were grown only with conspecifics, indicating that it is competitive ability that is primarily affected. Negative feedbacks affecting competitive ability, rather than growth in the absence of competition have rarely been directly investigated and this might have lead to a significant underestimation of the incidence and strength of Janzen-Connell effects in natural communities. We also failed to find effects on germination and seedling survival, although many studies of Janzen-Connell effects only examine these measures (Hyatt et al. 2003).

The almost complete removal of the negative feedback across the community by soil sterilization strongly suggests that soil biota were the primary agents causing the observed effects. These soil organisms must be host-specific (Freckleton and Lewis 2006) as generalist pathogens would be expected to affect plants growing at home and away equally. Pathogenic fungi are most often specifically examined in feedback studies and in some cases their effect has been directly demonstrated (Mills and Bever 1998, Packer and Clay 2000, Klironomos 2002). However, pathogenic fungi can be very variable in their host range (Augspurger and Wilkinson 2007) and very often information about host-specificity is lacking (Freckleton and Lewis 2006). In our study, we were unable to attribute the effect to soil fungi. While absolute plant biomass increased on both home and away soils with the addition of fungicide, it increased more strongly on away soils, intensifying the net negative feedback (Fig. 1). The most likely explanation is that generalist pathogenic fungi constrained other, even more detrimental, soil organisms (e.g., bacteria, or specific fungicide-tolerant fungi or fungus-like organisms such as Oomycetes). In a separate experiment, Zeller et al. (2007) showed that the biomass of the species with the greatest negative soil feedback, *Echinochloa crus-galli*, is reduced by 90% when infected with a cyanide-producing *Pseudomonas* bacterial strain. Other soil organisms that could be responsible for the negative feedback include nematodes and larger invertebrates such as insect larvae (De Deyn et al. 2003).

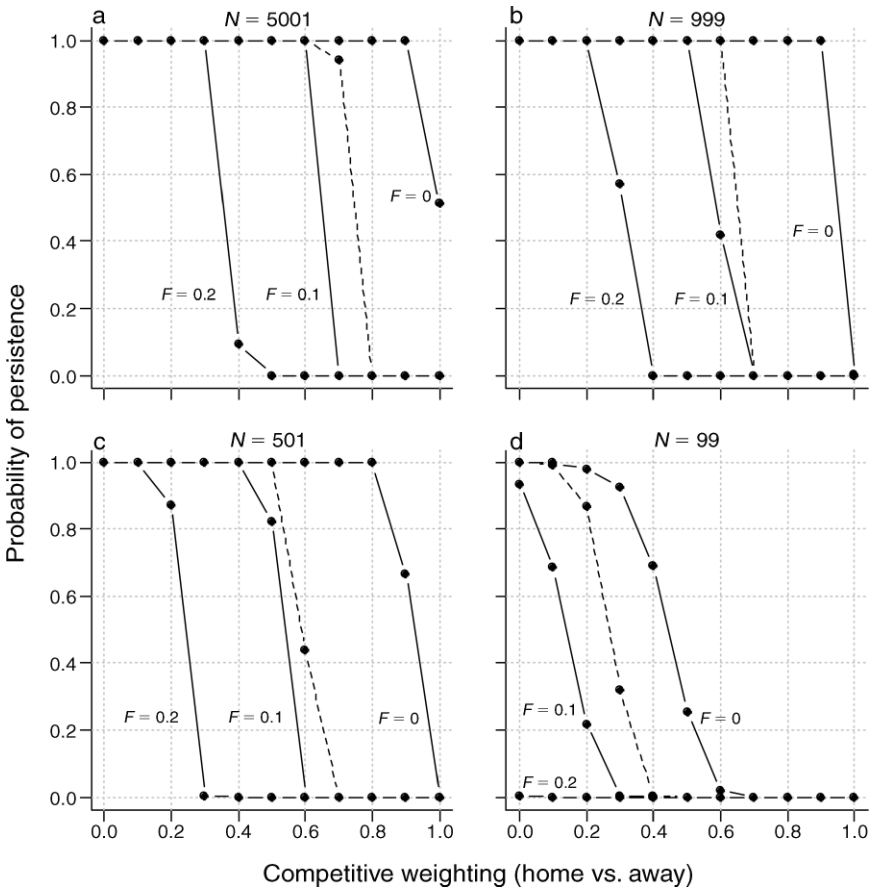

FIG. 3. Community dynamics with and without negative soil feedbacks: in a community of fixed total size (N), the probability of all three functional groups persisting for 10 000 years decreases as the competitive weighting (home vs. away) increases, and as fitness differences (F) between functional groups increase from zero ($F = 0$) to 10% ($F = 0.1$) and 20% ($F = 0.2$). As the community size decreases from ~5000 to ~100 (a–d) a lower weighting (home vs. away) is needed to ensure persistence. Fitness differences are incorporated as differences in death rates. Model simulations using observed fitness differences between functional groups (average death rates over the summer) are also shown (dashed line). The competitive weighting (home vs. away) estimated in this experiment is 0.5.

In contrast to previous studies which have demonstrated dramatic negative effects caused by allelochemicals released by exotic plant invaders on native plant species (Callaway and Aschehoug 2000), we found no consistent chemically mediated effects. Thus, chemical weapons do not seem to play an important role in structuring communities of native species with a common evolutionary history. The fact that the negative feedback was to some extent reduced in samples treated with fertilizer implies that part of the negative soil feedback could have been due to specific nutrient depletion. This represents abiotic density dependence (Ehrenfeld et al. 2005) and corresponds to predictions from classical resource niche theory (Tilman 1982). On the other hand, fertilizer addition could simply have mitigated the detrimental effect of pathogenic soil organisms by removing nutrient limitation (van der Putten and Peters 1997).

Several studies have examined feedback effects and their impact on community processes using deterministic models and have identified conditions for successful exotic invasion and the coexistence of species (e.g., Eppstein and Molofsky 2007). Here, we investigated the potential consequences of measured feedbacks on the persistence of three species each belonging to a different functional group in communities of different total size. In a community without negative feedbacks, the population dynamics are characterized by pure ecological drift and there is no stable equilibrium (Chesson 2000, Hubbell 2001). Although populations can persist for long periods under drift, this is only true when fitness differences are minimal (Zhang and Lin 1997). When fitness differences are present, stabilizing mechanisms, for example resource niches, are required (Chesson 2000); and the stronger the fitness inequalities, the stronger the stabilizing forces needed (Adler et al. 2007, Harpole and Suding 2007). We show that soil-mediated negative feedbacks can be potent stabilizing forces. The size of the measured feedbacks, coupled with information on typical fitness differences between the functional

groups, indicates that negative soil feedbacks could play an important role in the maintenance of functional diversity in grasslands, providing that seeds are dispersed sufficiently far from the parent sites.

In traditional niche theory, the number of species able to coexist in a community increases with the number of niche dimensions (Hutchinson 1978). Recently, this concept of "high-dimensional" coexistence has again gained favor (Clark et al. 2007). Here we show that Janzen-Connell effects could be an important source of niche-dimensionality, with "pathogen niches," or rather pathogen-free space, providing the resource axes. Similarly, studies of biodiversity and ecosystem functioning often conclude that resource partitioning causes diverse communities to outperform monocultures; however, Janzen-Connell effects could be an equally likely explanation of why monocultures "under perform" compared to mixtures (Mwangi et al. 2007). Soil-mediated Janzen-Connell effects might furthermore be the reason that monocultures are much more easily invaded than mixtures, as has been shown in numerous previous experiments (Hector et al. 2001, Mwangi et al. 2007).

Our results demonstrate that Janzen-Connell effects are widespread among the three major functional groups in European grasslands. Each functional group is consistently disadvantaged when competing for sites that it has formerly occupied, leading to natural rotations of site occupancies, similar to those traditionally imposed by farmers. Under a neutral model, a monoculture functions just as well as a diverse community; but if low-diversity communities quickly accumulate specialist soil pathogens, these depauperate communities may develop the same "soil sickness" which continues to plague some farmers today.

Acknowledgments

We thank G. de Deyn, A. Hector, D. W. Purves, W. van der Putten, and D. A. Wardle for discussions and comments. This research was supported by grant 31-65224.01 from the Swiss National Science Foundation to B. Schmid and L. A. Turnbull. J. S. Petermann and A. J. F. Fergus contributed equally to this work.

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APPENDIX A

Supplementary materials, methods, and tables (*Ecological Archives* E089-135-A1).

APPENDIX B

Mean soil feedback on seedling emergence (*Ecological Archives* E089-135-A2).

APPENDIX C

Design of the main experiment (*Ecological Archives* E089-135-A3).

APPENDIX D

The effect of seed dispersal on persistence time (*Ecological Archives* E089-135-A4).

Ecological Archives **E089-135-A1**

Appendix A. Supplementary materials, methods, and tables.

Soil origin and preparation
We used soils from 24 field monocultures (one per species), each measuring 1.5 × 2 m. We removed four subsamples of soil from the top 25 cm of each of the monocultures, insulated them against peak frosts and stored them outside for three months to mimic seasonal temperature changes. We mixed the soils by sieving (1 cm mesh width), removed stones, cut roots into 1.5 cm pieces and returned them to the soil.
Soils were either (1) sterilized by gamma irradiation (>25 kGray) to remove all soil organisms, (2) received twice the recommended dose of a broad-spectrum fungicide to remove all fungi (Carbendazim; Methyl-benzimidazol-2-ylcarbamat, Sintagro AG, Härkingen, Switzerland, 1.8 g/pot), (3) were mixed with activated carbon (washed with hydrochloric acid, Sigma-Aldrich, Switzerland, 2 % by volume) to remove allelochemicals or (4) were fertilized with a liquid NPK-fertilizer (Gesal, Compo Jardin AG, Allschwil, Switzerland, 110.7 mg/pot N (102.6 mg as carbamide and 8.1 mg as ammonium), 63.6 mg/pot P (as phosphoric acid), 180.0 mg/pot K (as potassium hydroxide) once at the beginning of the experiment. Nutrient concentrations were still significantly higher in the fertilizer treatment compared with the sterilization treatment at the end of the experiment (based on a subset of 9 soil types from 54 mixture pots (replicate pots were pooled): $F_{1,8}$ = 11.9, $P < 0.01$ for nitrogen and $F_{1,8} = 63.5$, $P < 0.001$ for phosphorus).

Experiment
The 24 species were grouped into eight sets, each containing one forb, one grass and one legume species (Table A2). Initially, species were grouped into four early- and four mid-successional sets with random assignment of species within functional group and successional stage. The factor "successional stage" was not significant ($F_{1,6} = 0.64$, $P = 0.451$, tested against "set" within the species term) and was dropped from the analysis. We surface-sterilized seeds with 7 % sodium-hypochlorite before the experiment. Plants were grown in the glasshouse under a 15/9h light/dark cycle (minimum light level 400 $\mu Em^{-2}s^{-1}$ during the day) and a mean temperature of 20°C (minimum 15°C, maximum 28°C). We watered all pots manually three times a week to keep soil moisture constant, avoiding any exchange of water between the pots. Pots were randomized every two weeks to remove spatial variation.

Supplementary Modeling: Incorporating local dispersal into the model framework

In the models presented in the main paper, we assume infinite fecundity and global dispersal. To incorporate local dispersal, we first need to make fecundity finite. The model also needs to be spatially explicit, with a grid of N patches which are fully occupied by the three functional groups. Some fraction (F) of the seeds produced by each individual remains within the local patch, while the remainder (1-F) is dispersed to form a global seed rain. All plants reproduce before mortality acts, thus the mean number of seeds of species i arriving in patch q at time t ($n_{i,q,t}$) follows a Poisson distribution, with mean equal to the sum of the within-patch and global dispersal terms:

$$\overline{n}_{i,q,t} = F.(R_i) + (1-F)R_i.N_i.(1/N)$$

where R_i is the reproductive output of an individual of species i. We chose $R_i = 100$ as this is typical of values found for grassland plants, and creates a suitable degree of stochasticity in the seed inputs. Otherwise the model is the same as described in the main paper with parameter values taken from the experimental and field data, i.e., $c_{ii}= 0.5$ for all i, $c_{ij}= 1$ for all i and j and $d_{legume} = 0.466$, $d_{grass}= 0.450$, $d_{forb}= 0.364$. We varied F in the range 0 – 1 in steps of 0.1 ($F = 1$ corresponds to full global dispersal). For each value in this range, the mean persistence time of all three functional groups was calculated from 100 runs each of 10,000 generations.

Local dispersal does indeed have dramatic consequences for the persistence of the three functional groups (Fig. D1). Only when $F \leq 0.7$ do the three functional groups persist for 10,000 generations. When $F = 0.6$, the three groups persist on average for around 6,000 years, but with $F \leq 0.5$, the functional group with the lowest fitness only persists on average for 2,000 years (and never persists for 10,000 years). This occurs because seeds are increasingly concentrated in patches where recruitment probability is low. This highlights the importance of dispersal away from the parent site when Janzen Connell effects or negative soil feedbacks operate. This is particularly true when species have unequal fitness, as the species with the lowest fitness must ensure that it disperses seeds into sites where it has a better chance of recruiting.

Supplementary Tables

TABLE A1. Results from the mixed-model ANOVA for log-ratio of biomass (biomass of individual plants on home soils divided by biomass of individuals on away soils for each species, log-transformed). The species term (bold) is split into one contrast (normal print), the row numbers of the respective error terms are given in the last column (fixed effects are tested against random effects, random effects against the residual).

Source of variation	df	*F*	*P*	Error term
1 Mean	**1**	**35.69**	**<0.001**	**4**
2 Competition	**1**	**16.68**	**<0.001**	**6**
3 Functional group of soil	**2**	**0.47**	**0.634**	**7**
4 Species	**23**	**12.33**	**<0.001**	**11**
4a Functional group	2	0.53	0.595	4b
4b Species	21	12.86	<0.001	11
5 Treatment	**4**	**4.68**	**0.002**	**8**
6 Competition × Species	**23**	**6.55**	**<0.001**	**11**
7 Functional group of soil × Species	**22**	**4.08**	**<0.001**	**11**
8 Species × Treatment	**92**	**10.24**	**<0.001**	**11**
9 Competition × Treatment	**4**	**9.59**	**0.010**	**10**
10 Competition × Species × Treatment	**91**	**1.67**	**0.001**	**11**
11 Residuals	**215**			
Total	478			

TABLE A2. The 24 species were grouped into eight experimental sets, each containing one grass, one forb and one legume of the same successional stage. Assignment of species to sets within successional stage and functional groups was random. Each species was then grown on home (soil from same species) and away soils (soils from the other two species in the set) either in monoculture or in competition with the other species in its set.

Set	Species	Functional group	Successional stage
1	*Panicum capillare*	GRASS	
	Lepidium campestre	FORB	early
	Trifolium incarnatum	LEGUME	
2	*Bromus sterilis*	GRASS	
	Arctium tomentosum	FORB	early
	Trifolium campestre	LEGUME	
3	*Echinochloa crus-galli*	GRASS	
	Berteroa incana	FORB	early
	Melilotus albus	LEGUME	
4	*Hordeum murinum*	GRASS	
	Tanacetum vulgare	FORB	early
	Vicia villosa	LEGUME	
5	*Arrhenaterum elatius*	GRASS	
	Plantago lanceolata	FORB	mid
	Medicago lupulina	LEGUME	
6	*Holcus lanatus*	GRASS	
	Centaurea jacea	FORB	mid
	Trifolium pratense	LEGUME	
7	*Festuca rubra*	GRASS	
	Leucanthemum vulgare	FORB	mid
	Vicia cracca	LEGUME	
8	*Dactylis glomerata*	GRASS	
	Galium mollugo	FORB	mid
	Trifolium repens	LEGUME	

TABLE A3. Results from a mixed-model ANOVA of log-ratio of seedling emergence (seedling emergence probability on home soils divided by seedling emergence probability on away soils, ratio log-transformed), random effects were the species term and its interaction, fixed effects were the overall mean and the treatment, they were tested against random effects. There was no competition treatment for seedling emergence.

Source of variation	df	*F*	*P*	Error term
1 Mean	**1**	**0.24**	**0.627**	**2**
2 Species	**23**	**11.78**	**<0.001**	**5**
3 Treatment	**4**	**0.81**	**0.524**	**4**
4 Species × treatment	**91**	**1.76**	**0.002**	**5**
5 Residual	**119**			
Total	237			

Appendix B. Mean soil feedback on seedling emergence.

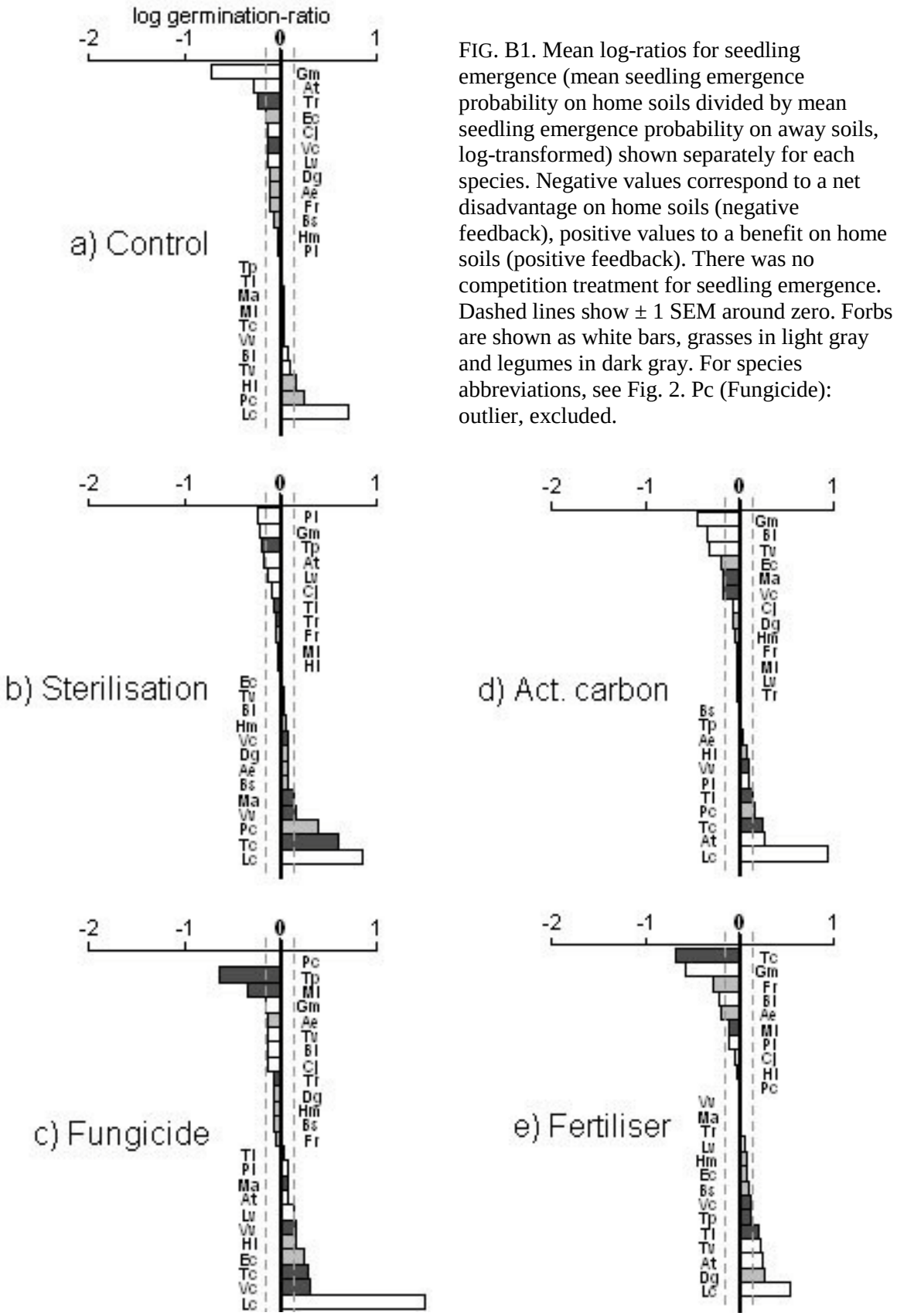

FIG. B1. Mean log-ratios for seedling emergence (mean seedling emergence probability on home soils divided by mean seedling emergence probability on away soils, log-transformed) shown separately for each species. Negative values correspond to a net disadvantage on home soils (negative feedback), positive values to a benefit on home soils (positive feedback). There was no competition treatment for seedling emergence. Dashed lines show ± 1 SEM around zero. Forbs are shown as white bars, grasses in light gray and legumes in dark gray. For species abbreviations, see Fig. 2. Pc (Fungicide): outlier, excluded.

Appendix C. Design of the main experiment.

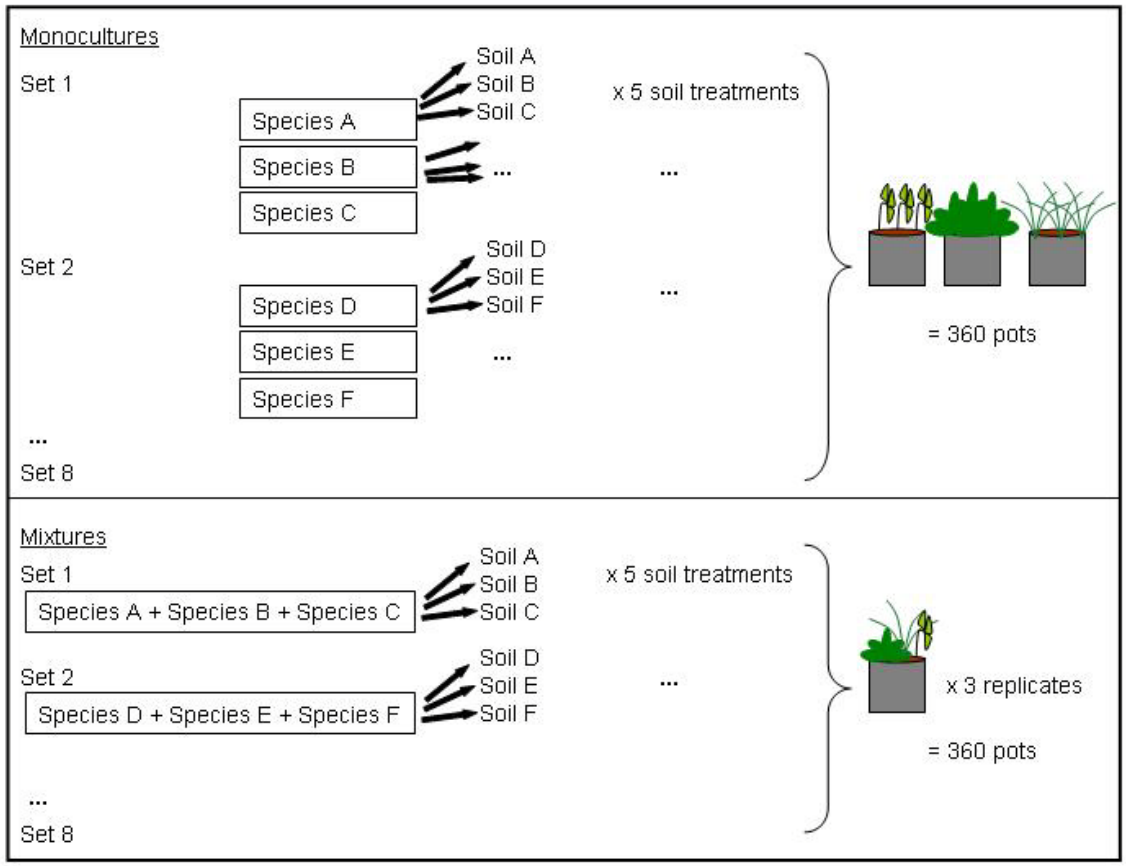

FIG. C1. Design of the main experiment: 24 species were grouped into 8 sets with one representative of each functional group (see Appendix A Table A2). For the monospecific communities ("Monocultures"), three individuals per pot were grown for each species on the three soils in its set (including its own). These 72 combinations were crossed with five soil treatments, adding up to a total of 360 pots. Multi-species communities ("Mixtures") were assembled by using one individual of each of the three species in the set per pot. This community was grown on each soil of the set, in five soil treatments. Because there were three replicates of each combination, there were also 360 mixture pots in the experiment.

Appendix D. The effect of seed dispersal on persistence time.

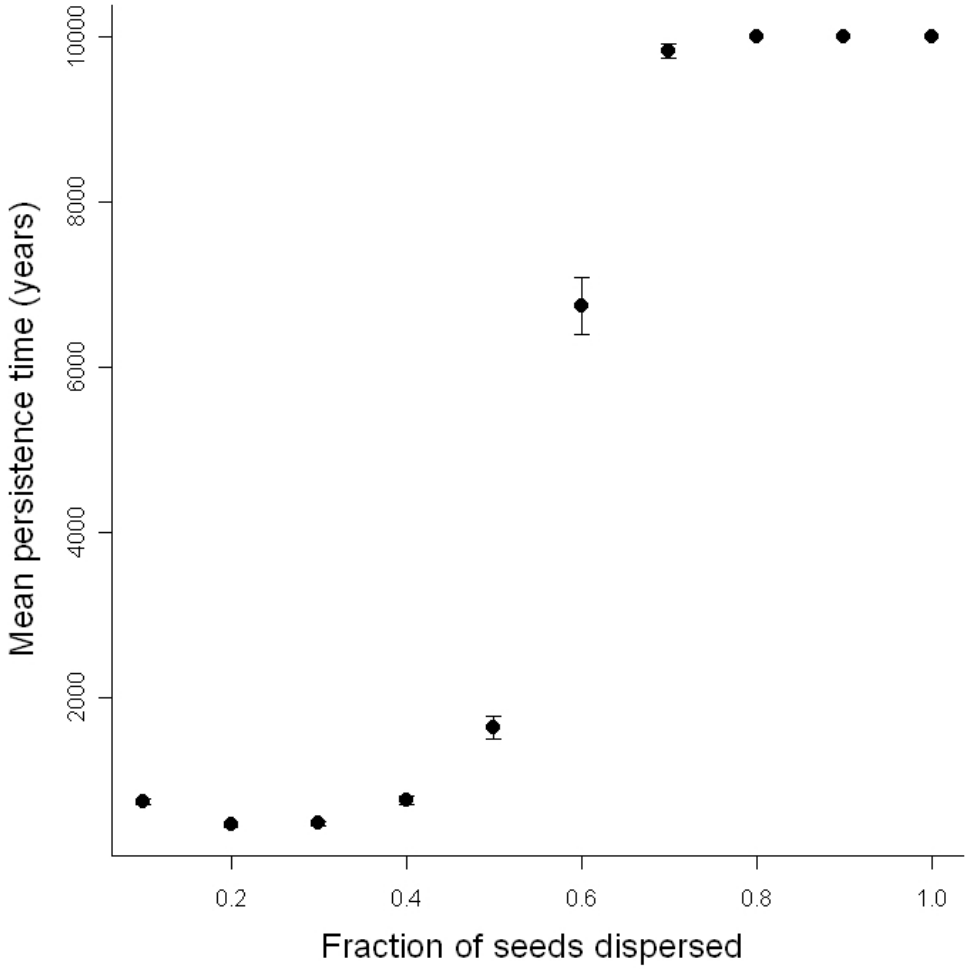

FIG. D1. The effect of increasing the fraction of seeds dispersed away from the parent site on mean persistence time. For other model parameters see text.

CHAPTER 2

Species diversity reduces invasion success in pathogen-regulated communities

Turnbull LA, Levine JM, Fergus AJF, Petermann JS, *Oikos* in press

"*So you can imagine what happens when a mainland species gets introduced to an island. It would be like introducing Al Capone, Genghis Khan and Rupert Murdoch into the Isle of Wight - the locals wouldn't stand a chance.*" (Adams and Carwardine 1991)

Abstract

The loss of natural enemies is thought to explain why certain invasive species are so spectacularly successful in their introduced range. However, if losing natural enemies leads to unregulated population growth, this implies that native species are themselves normally subject to natural enemy regulation. One possible widespread mechanism of natural enemy regulation is negative soil feedbacks, in which resident species growing on home soils are disadvantaged because of a build-up of species-specific soil pathogens. Here we construct simple models in which pathogens cause resident species to suffer reduced competitive ability on home soils and consider the consequences of such pathogen regulation for potential invading species. We show that the probability of successful invasion and its timescale depend strongly on the competitive ability of the invader on resident soils, but are unaffected by whether or not the invader also suffers reduced competitive ability on home soils (i.e. pathogen regulation). This is because, at the start of an invasion, the invader is rare and hence mostly encounters resident soils. However, the lack of pathogen regulation does allow the invader to achieve an unusually high population density. We also show that increasing resident species diversity in a pathogen-regulated community increases invasion resistance by reducing the frequency of home-site encounters. Diverse communities are more resistant to invasion than monocultures of the component species: they preclude a greater range of potential invaders, slow the timescale of invasion and reduce invader population size. Thus, widespread pathogen regulation of resident species is a potential explanation for the empirical observation that diverse communities are more invasion resistant.

Introduction

The loss of pathogens, herbivores and predators is commonly believed to underlie the success of some exotic plant species in their introduced range (the enemy release hypothesis: Elton 1958, Keane and Crawley 2002, Mitchell and Power 2003, Torchin and Mitchell 2004, Theoharides and Dukes 2007). However, if the loss of natural enemies is presumed to cause unregulated population growth, this implies that native species normally experience natural enemy regulation. This contrasts with the prevailing view of many plant community ecologists who have traditionally emphasised resource-based mechanisms of coexistence (Tilman 1982, Grime 2001, Tilman et al. 2001, Cardinale et al. 2007).

Recent empirical work has shown that native plant species often suffer from negative soil feedbacks, a type of density-dependent regulation imposed by species-specific soil herbivores and pathogens (van der Putten et al. 1993, Bever 1994, Klironomos 2002, De Deyn

et al. 2003, Bartelt-Ryser et al. 2005, Kardol et al. 2006). After a given plant species occupies a site for some time, specialist soil pathogens accumulate and reduce the performance of conspecific plants in subsequent generations – a type of Janzen-Connell effect (Janzen 1970, Connell 1971). The strength of these feedbacks is usually measured by comparing the performance of individuals on soils formerly occupied by the same species (home sites) or on soils formerly occupied by other species (away sites). Negative feedbacks have been reported from a variety of communities and vary considerably in strength (Kulmatiski et al. 2008). For example, in field-trained soils, Petermann et al. (2008) found that species from three different functional groups only achieved half the biomass on home soils versus away soils when grown in competition with other functional groups, although others have found weaker effects (Engelkes et al. 2008). Thus, pathogen regulation – in the form of negative soil feedbacks – is sufficiently widespread to warrant serious consideration as an alternative to resource-based mechanisms of coexistence (Kulmatiski et al. 2008, Petermann et al. 2008).

Invasive plants in their introduced range have often been found to suffer weaker negative soil feedbacks than their native competitors, suggesting that a lack of regulation by soil pathogens could be critical to their success (Klironomos 2002, Callaway et al. 2004, but see Beckstead and Parker 2003, Eppinga et al. 2006). For example, some have argued that freedom from negative feedbacks aids expansion of species into new territory (van Grunsven et al. 2007, Engelkes et al. 2008, Menendez 2008, but see Levine et al. 2006 and Eppstein and Molofsky 2007). However, because invaders must begin from low population density where home-site encounters are rare, we hypothesise that freedom from negative feedbacks is unlikely to increase the probability of successful invasion. We instead believe that the key ingredient to successfully invading resident communities is good competitive ability on resident soils.

We also hypothesise that soil pathogen regulation might interact with resident species diversity to influence invasion success. If negative feedbacks act on resident species then monocultures are likely to be particularly susceptible to invasion: in monocultures, resident species *only* encounter home sites where their performance is weakest. In contrast, in diverse communities, each resident species provides away sites on which the remaining residents can compete strongly; hence resident species in diverse communities largely avoid negative soil feedbacks. We might therefore expect that an invader would find it more difficult to invade diverse pathogen-regulated communities. This is consistent with a large body of empirical evidence showing that more diverse communities are indeed more difficult to invade (Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001, Fargione et al. 2003, van Ruijven et al.

2003, Levine et al. 2004). While such results are usually attributed to more complete resource use in diverse communities, the role of soil feedbacks in explaining these patterns has not been explored.

Here we use simple models to explore the requirements for successful invasion when the resident plant community is regulated by negative soil feedbacks. We focus on simulation models because analytical solutions for multi-species systems are difficult, although we do provide analytical support for our invasion conditions (for a detailed theoretical treatment of the two-species case see Eppstein and Molofsky 2007). We first examine the impact of changing the strength of the negative feedback experienced by the invader on its probability of invasion, its rate of population increase and its equilibrium abundance. Second, we consider the effect of changing resident diversity on these same three measures of invasion success.

Methods and Results

We consider invasion into a community of 100,000 sites each occupied by a single adult plant, whose dynamics are governed by a weighted lottery (Chesson & Warner 1981). Each year all plants in the community produce the same number of seeds, suffer the same probability of mortality (d_i = 0.2) and compete for the sites vacated by the death of adults. The proportion of newly-vacated sites won by a given species is proportional to the product of its relative abundance in the community and its competitive ability, α. The value of α varies between the invader (denoted by an *i* subscript) and the resident (denoted by an *r* subscript) and between home and away soils, generating four values: $\alpha_{i,\text{home}}, \alpha_{i,\text{away}}, \alpha_{r,\text{home}}, \alpha_{r,\text{away}}$. Sites thereby carry a memory of the former occupant which influences future competitive interactions on that site. Based on the findings of Petermann *et al.* (2008), we assume that pathogen-driven negative soil feedbacks reduce competitive ability by half on home soils. Thus, for all simulations, we arbitrarily set the competitive ability of the resident species on away soils, $\alpha_{r,\text{away}}$ to be 0.4, and the competitive ability of the resident species on its home soil to exactly half this value, $\alpha_{r,\text{home}} = 0.2$.

To examine the influence of invader competitive ability on its success, we varied invader performance on away soils, $\alpha_{i,\text{away}}$, over the interval 0.15 - 0.85 in steps of 0.05. A frequency-independent increase in competitive ability such as this is one possible advantage of escaping soil pathogens. The other possibility is escape from frequency or density-dependent regulation imposed by negative soil feedbacks. To examine the effects of invader

feedbacks on invader success, the invader either experienced no negative soil feedback: $\alpha_{i,\text{home}} = \alpha_{i,\text{away}}$ or, the invader suffered the same magnitude of negative soil feedback as the residents: $\alpha_{i,\text{home}} = 0.5 * \alpha_{i,\text{away}}$.

For simplicity, dispersal is global, meaning that the chance of a given species winning a site is a function of its proportion in the community at large, not its local proportion. Strongly limited dispersal would undoubtedly affect model outcomes (Eppstein & Molofsky 2007); however, we previously found that results were unaffected by the inclusion of local dispersal as long as > 50% of the seeds produced by each parent disperse away from the parent site (Petermann *et al.* 2008). All invasions were initiated with 16 invader individuals (~ 0.02 % of the community). For each implementation of the model we recorded 1) whether or not the invasion succeeds; 2) the number of generations required for the invader to reach 1000 individuals (1 % of the total community) and 3) the final population size of both the resident and the invader. An invasion is judged successful if at least one individual remains after 2000 generations following introduction. For any given set of parameters, we performed 1000 repeated runs from identical starting conditions.

Invasion into a system with a single resident species.

In a monoculture, all sites initially consist of home sites for the resident, while a rare invader initially encounters only away sites. As a consequence, whether or not the invader itself possesses a negative feedback has a negligible effect on its probability of successful invasion or the time required to reach 1000 sites (Figs. 1a & b). Of much greater importance is the invader's general competitive ability ($\alpha_{i,away}$), which strongly increases its probability of success (Fig. 1a) and decreases the time required to reach 1000 individuals (Fig. 1b).

However, should the invader satisfy the condition for successful invasion, the equilibrium population size of the invader is much larger when the invader lacks its own negative feedback (Fig. 1c). The equilibrium abundance of the invader is determined by the relative competitive abilities of the invader and the resident on home and away soils (Fig. 1c). For $0.2 < \alpha_{i,\text{away}} < 0.4$ the two species coexist, even when the invader lacks pathogen regulation; although without pathogen regulation the invader is more abundant than the resident. Similarly, an invader without pathogen regulation can exclude the resident when $\alpha_{i,\text{away}} > 0.4$, because it can outcompete the resident on both home and away sites (the resident's competitive ability never exceeds 0.4). However, a pathogen-regulated invader requires a higher minimum competitive ability on resident soils to exclude the resident,

$\alpha_{i,\text{away}} > 0.8$. All of these thresholds can be analytically derived for this model, as shown below.

Analytical conditions for invasion and impact

The simulation results are supported by analytical equations describing the same dynamics but over an infinitely large number of sites. The proportion of sites occupied by the invader, p_i, changes from one time step to the next as follows:

$$p_{i,t+1} = (1-d)p_{i,t} + d\left[p_{i,t} \frac{\alpha_{i,\text{home}} p_{i,t}}{\alpha_{i,\text{home}} p_{i,t} + (1-p_{i,t})\alpha_{r,\text{away}}} + (1-p_{i,t}) \frac{\alpha_{i,\text{away}} p_{i,t}}{\alpha_{i,\text{away}} p_{i,t} + (1-p_{i,t})\alpha_{r,\text{home}}} \right] \quad (1)$$

The first term of the sum describes the proportion of invader individuals surviving over the time step, while the second term is the proportion of newly-vacated sites subsequently filled by the invader. The proportion of newly-vacated sites filled by the invader is a weighted average of dynamics on sites that were formerly occupied by the invader (the first term of the bracketed sum) and dynamics on sites formerly occupied by the resident (the second term of the bracketed sum). The invader wins sites in proportion to the product of its abundance and competitive ability, relative to the product of these values for the resident.

To obtain the condition for the invader to increase from rarity, we divide both sides of equation one by $p_{i,t}$, yielding the per capita growth rate for the invader:

$$\frac{p_{i,t+1}}{p_{i,t}} = (1-d) + d\left[p_{i,t} \frac{\alpha_{i,\text{home}}}{\alpha_{i,\text{home}} p_{i,t} + (1-p_{i,t})\alpha_{r,\text{away}}} + (1-p_{i,t}) \frac{\alpha_{i,\text{away}}}{\alpha_{i,\text{away}} p_{i,t} + (1-p_{i,t})\alpha_{r,\text{home}}} \right] \quad (2)$$

When the invader is rare, $p_{i,t}$ is near zero, simplifying the growth rate to:

$$\frac{p_{i,t+1}}{p_{i,t}} = (1-d) + d\left[\frac{\alpha_{i,\text{away}}}{\alpha_{r,\text{home}}} \right] \quad (3)$$

For the invader to increase when rare, this growth rate must exceed one, and simplifying yields the invasion condition:

$$\alpha_{i,\text{away}} > \alpha_{r,\text{home}} \quad (4)$$

Thus, the invader can successfully increase when rare if it can outcompete the resident on the resident's home soil. Importantly, condition 4 does not contain $\alpha_{i,\text{home}}$ and hence a negative feedback for the invader will not affect its probability of successful invasion or its dynamics when rare (Fig. 1a & 1b). Condition 4 also explains why the threshold for successful invasion in the simulations is $\alpha_{i,\text{away}} > 0.2$ ($\alpha_{r,\text{home}} = 0.2$ in the simulations).

Equations 1-4 above can also be used to describe the dynamics of the resident species by switching the *i* and *r* subscripts. We can thus derive the condition for the resident to persist with the invader (as the resident must also be able to increase when rare). This reveals that the resident can increase when rare as long as $\alpha_{r,\text{away}} > \alpha_{i,\text{home}}$. Thus the invader can displace the resident in our simulations when $\alpha_{i,\text{home}} > 0.4$. Notice that, this requires $\alpha_{i,\text{away}} > 0.8$ if the invader possesses the same negative feedback as the resident ($\alpha_{i,\text{home}} = 0.5 * \alpha_{i,\text{away}}$); however if the invader does not possess a negative feedback, displacement of the resident occurs when $\alpha_{i,\text{away}} > 0.4$ (Fig. 1c).

Invasion into more diverse communities

It is clear from above that monocultures are particularly susceptible to invasion because all sites are home sites for the resident. However, if the resident community contains more than one species, each suffering from its own specialist soil pathogens, then a greater fraction of newly-vacated sites are away sites for each of the resident species. To evaluate this effect of resident diversity, we simulated models containing 1, 2, 4, 8 and 16 resident species. In each case, we assumed that all resident species have exactly the same competitive ability on away soils: $\alpha_{r,\text{away}} = 0.4$, and that they all suffer a negative soil feedback of the same magnitude: $\alpha_{r,\text{home}} = 0.2$. This strongly stabilizes dynamics such that residents would coexist indefinitely and at identical abundances were it not for the finite community size.

In our multi-resident simulations, all residents begin at equal proportions, and are given 500 generations of dynamics prior to the introduction of the invader to 16 sites taken equally from the resident species. We varied the competitive ability of the invader on away soils over the interval 0.20 to 0.50 in steps of 0.025. We use a narrower interval with finer gradations than in the previous simulations, as it is clear that once $\alpha_{i,\text{away}} > 0.4$ the invader is a better competitor than all members of the resident community ($\alpha_{i,\text{away}} > \alpha_{r,\text{home}}$). We only consider the case where the invader also suffers from a negative soil feedback, which again, is identical in magnitude to that of the residents ($\alpha_{i,\text{home}} = 0.5 * \alpha_{i,\text{away}}$).

As hypothesized, increasing resident diversity increases the minimum competitive ability required for successful invasion (Fig. 2a), increases the time-scale of the invasion (Fig. 2b) and reduces the population size of successful invaders (Fig. 2c). The minimum competitive ability on resident soils required for successful invasion increases asymptotically with increasing resident diversity (Fig. 3a), so the largest change is seen when moving from a

monoculture to a 2-species mixture and each additional resident species has an increasingly small effect (we demonstrate this point analytically below). We therefore predict that weaker competitors are precluded from invading more diverse mixtures, even though they can invade monocultures of all the constituent species. For any given invader, the final population size also declines monotonically with increasing resident species diversity (Fig. 3b), although the time to reach 1000 individuals (the growth rate when rare) increases linearly with species diversity (Fig. 3c). Thus, the different components of invasion success scale differently with increasing resident diversity.

The effects of resident species diversity on invasion success can be shown analytically. If the community contains *D* identical pathogen-regulated residents, each resident will hold 1/*D* of the sites not occupied by the invader. Thus, on newly-vacated resident sites, 1/*D* of the colonizing residents have competitive ability given by $\alpha_{r,\text{home}}$ and (*D*-1)/*D* of the colonizing residents have competitive ability given by $\alpha_{r,\text{away}}$. We thus replace the resident performance in the second term of the bracketed sum in Equation 1 with the following:

$$\left(1-p_{i,t}\right)\left(\frac{\alpha_{i,\text{away}}}{\alpha_{i,\text{away}}p_{i,t}+\left(\frac{1}{D}\right)\left(1-p_{i,t}\right)\alpha_{r,\text{home}}+\left(\frac{D-1}{D}\right)\left(1-p_{i,t}\right)\alpha_{r,\text{away}}}\right) \qquad (5)$$

The condition for the invader to increase when rare now becomes:

$$\alpha_{i,\text{away}} > \alpha_{r,\text{away}}\left(\frac{D-1}{D}\right)+\alpha_{r,\text{home}}\frac{1}{D} \qquad (6)$$

Condition 6 reveals that the invader's competitive ability on away soils must exceed a weighted average of the residents' competitive abilities on home and away soils. With *D* = 1 (a monoculture), the first term of the sum disappears and we return to condition 4. As diversity (*D*) increases, the second term of the sum decreases, and because $\alpha_{r,\text{away}} > \alpha_{r,\text{home}}$, invasion becomes more difficult. Also notice that the greatest decrease in the weighting of $\alpha_{r,\text{home}}$ (and hence the greatest change in invasion resistance) occurs when *D* goes from 1 to 2, matching simulations in Fig. 2a & 2b.

Discussion

The loss of natural enemies has often been implicated in the success of exotic species in their introduced range (Keane and Crawley 2002) while the inevitable corollary – that plant populations normally experience natural enemy regulation in their native range – has been largely overlooked. One possible general mechanism for this regulation is negative plant-soil

feedbacks, where species are disadvantaged on previously-occupied or home sites, analogous to the Janzen-Connell effect. There is widespread empirical evidence for species-specific negative soil feedbacks within plant communities, including evidence that exotic species experience weaker negative feedbacks than native species (Bever 1994, van der Putten and Peters 1997, Klironomos 2002, Bartelt-Ryser et al. 2005, Bonanomi et al. 2005). Several authors have therefore suggested that release from negative feedbacks may allow species to become invasive (van Grunsven et al. 2007, Engelkes et al. 2008).

We used a simple modelling approach to evaluate the potential benefit of escaping regulation by specialist soil pathogens. We found that the loss of a negative soil feedback has no influence on whether or not a given species is able to invade a resident community. Freedom from negative soil feedbacks alone cannot, therefore, allow a species to expand its range or enter new communities. Instead, the probability of successful invasion depends strongly on the competitive ability of the invader on resident soils. This is because, at the start of an invasion, the invader is at low density and so it mainly encounters resident sites. While limited dispersal inevitably changes this outcome to some degree (Bolker and Pacala 1999, Eppstein and Molofsky 2007), it seems unlikely that an invader will be successful if it cannot compete strongly against the residents on resident soils. Invader competitive ability on resident soils is also the primary determinant of the invader growth rate when rare; hence increased competitive ability on away sites also leads to more rapid invasion.

In contrast, if all resident species are affected by a generalist soil pathogen to which an invader is immune (a different form of enemy release), then this could give an invader a competitive advantage on resident soils. Hence, this type of enemy release could increase the probability of invasion success; however, in this case the invader has become successful, not through the loss of regulation, but rather because it has acquired a large fitness differential with respect to resident competitors. Such an effect would be better quantified by comparing the competitive ability of residents vs. the invader on sterilised and non-sterilised soil from the introduced range. Notice that in this case we are assigning a rather different role to pathogens in native communities, instead of being species-specific and providing regulation and stabilisation, they have an equalising role by having a general negative effect on all residents (Chesson 2000). A similar effect is proposed to occur if species lose specialist pathogens or herbivores and as a result are able to evolve increased competitive ability – the EICA hypothesis (Blossey & Notzold, 1995).

Invaders freed from negative soil feedbacks tend to achieve higher population densities once successful and are more likely to exclude resident species (Levine et al. 2006,

Eppstein and Molofsky 2007). Exclusion of residents is still possible when the invader possesses pathogen regulation, should the invader compete strongly enough on all soil types; however, without pathogen regulation, the invader can reach higher abundance than the resident despite being a poorer competitor on away soils. Comparisons of performance on 'average' soil, compost mixes, or even the invader soil, would therefore be unrevealing. This emphasises the need for carefully controlled experiments on different soil types. Notice that although we used a strong feedback for our simulations, weak negative feedbacks give qualitatively similar results.

Monocultures of resident species which suffer negative soil feedbacks are particularly susceptible to invasion. In a monoculture, all sites are home sites for the resident, reducing the resident's average competitive ability across all available sites. Increasing resident diversity increases community resistance because many of the available sites are now away sites for each of the resident species. This raises the collective competitive ability of the resident community and makes the system more difficult to invade. Increasing resident diversity has diminishing returns; an asymptotic relationship emerged between resident diversity and invader establishment probability. In our models, resident species have identical characteristics, so that the increased invasion resistance of diverse communities is not due to a 'selection' effect by which mixtures are more likely to include species with particularly high resistance to invaders (Loreau and Hector 2001). Thus, a species which cannot invade a diverse mixture could potentially invade monocultures of all the constituent species.

The literature on invasion success in experimental manipulations of biodiversity reveals several patterns consistent with our results. First, the number of invading species and total invader biomass decrease with resident diversity in a non-linear way (Tilman 1997, Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001, Fargione et al. 2003) and second, several biodiversity experiments report that monoculture performance often declines with time (Pfisterer et al. 2004, Fargione et al. 2007). Although pathogens have not been directly implicated in either of these results, our models suggest that they could play some role. Many biodiversity experiments also reveal that functional group diversity is as important as species diversity in determining ecosystem functioning (Tilman et al. 1997, Hector et al. 1999, Hooper and Dukes 2004, Spehn et al. 2005). Although our models assumed that species possess unique pathogens, such results could be explained if species within the same functional or taxonomic group share pathogens (De Deyn et al. 2003, Gilbert and Webb 2007). For example, the increasing success of phylogenetic distance in explaining a variety of ecosystem performance measures (e.g. Cadotte et al. 2008) could also be attributed to

pathogens that cross-infect closely-related hosts, as could the observation that species are more successful in invading communities from which their own functional group is absent (Fargione et al. 2003, Turnbull et al. 2005).

Plant ecologists have tended to overlook natural enemies in favour of resource-based explanations for community dynamics and structure (see e.g. Harpole and Tilman 2007). However, a considerable body of evidence now demonstrates that pathogens, although often unseen, can have large and predictable effects on resident fitness (e.g. van der Heijden et al. 2008). Negative soil feedbacks in particular can act in a frequency-dependant manner to promote diversity (Bever 2003) and, as we have shown here, could also endow diverse pathogen-regulated communities with increased invasion resistance.

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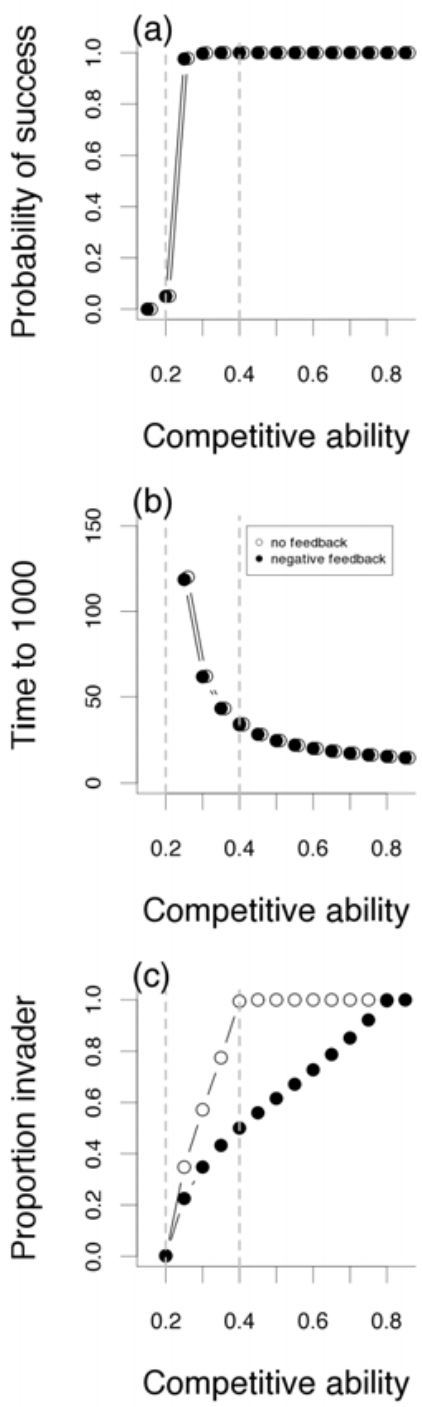

Figure 1: Success of an invader with and without a negative soil feedback and with different competitive abilities on 'away' soils. The probability that the invasion succeeds (a), the time-scale of successful invasion (b) and the proportion invader should the invasion succeed (c) are shown. Dashed lines show the competitive ability of the single resident species on home (0.2) and away soils (0.40). All values are calculated from 1000 repeated runs. The invader population size was calculated 2000 generations after introduction using data from successful invasions only (success constitutes >1 individual after 2000 generations). The timescale is the number of generations required for the invader to reach 1000 individuals.

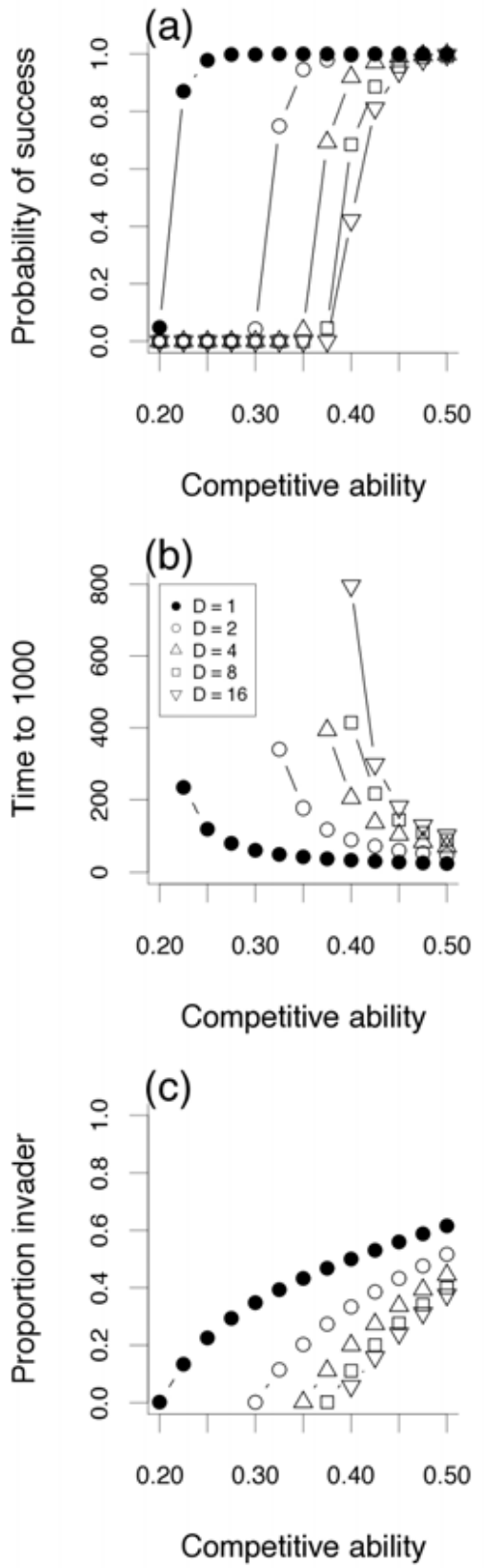

Figure 2: Success of an invader introduced into resident communities of different species diversity (D = 1, 2, 4, 8, 16). The resident species always have the same competitive ability on away soils (0.4) and on home soils (0.2). The probability that the invasion succeeds (a), the time-scale of successful invasion (b) and the final abundance of the invader (c) are shown.

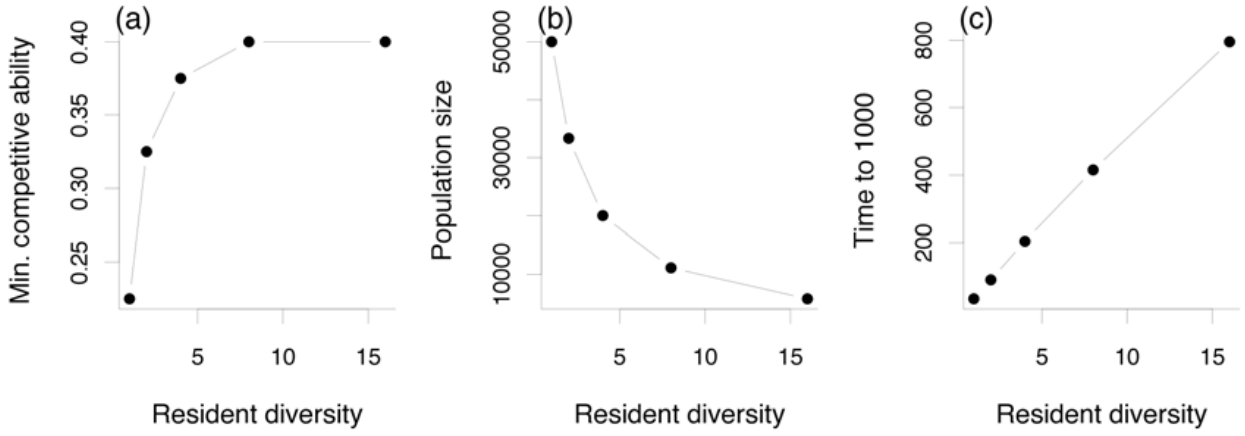

Figure 3: The relationship between resident diversity and the minimum competitive ability required for successful invasion (a). For an invader with exactly the same properties as the resident species, the population size of the invader (b) and the time required to reach 1000 individuals (c) are also shown.

CHAPTER 3

Biology, chance or history? The predictable re-assembly of temperate grassland communities

Petermann JS, Fergus AJF, Roscher C, Turnbull LA, Weigelt A, Schmid B, *Ecology* in press

"*When Prof. Buckland, the eminent osteologist and geologist, discovered that the relics of St. Rosalia at Palermo, which had for ages cured diseases and warded off epidemics, were the bones of a goat, this fact caused not the slightest diminution in their miraculous power*."
(White 1896, cited in Simberloff and Boecklen 1981)

"*One way to view progress in science is what occurs when variation moves from… (the error term) to…(the explanatory term).…The more we learn about a process, the 'less stochastic' it becomes.*"
(Clark 2009)

Abstract

Many studies have examined invasion resistance in plant communities, but few have explored the mechanisms of invasion and how subsequent community re-assembly affects community functioning. Using natural dispersal and deliberate seed addition into grassland communities with different compositional and richness histories, we show that invaders establish in a non-random manner due to negative effects of resident functional groups on invading species from the same functional group. Invaders hence complement communities with originally low richness levels. Consequently, communities converge toward similar levels of species richness, high functional richness and evenness, but not always maximum productivity. Invasion processes are faster but qualitatively similar when the effect of chance, in the form of dispersal stochasticity, is reduced by seed addition. Thus, dispersal limitation may influence community assembly but it does not override functionally predictable assembly mechanisms. Some of the most productive communities prior to invasion are unstable in the face of invasion, leading to decreased productivity following invasion. We suggest that invasion into such communities occurs possibly because a pathogen-free niche is available rather than a resource niche. Thus, pathogens in addition to resource niches may be important biological drivers of community assembly.

Introduction

Biology, chance and history must all play some role in community assembly. For example, in order to successfully establish in a new community, a potential invader must first arrive, and dispersal is an inherently stochastic process. However, the relative importance of dispersal limitation and historical contingency versus deterministic biological interactions is still hotly debated (e.g. Drake 1991, Hubbell 2001, Chase 2003, Fargione et al. 2003, Turnbull et al. 2005a, Turnbull et al. 2005b).

The first explanations as to why certain species were able to successfully invade new communities were certainly deterministic in nature and focussed mainly on the biology of the invaders (see e.g. Elton 1958). For instance, some species appeared to be more successful than others at dispersing to new sites, at entering new communities or at reaching high population sizes and suppressing residents (Crawley 1986, Drake et al. 1989). This observation led to a focus on the properties of these species and their associated "invasiveness" (Baker 1967, Sutherland 2004, Richardson and Pysek 2006).

Conversely, invasion success might be related to the biology of the invaded or resident community; for example, more diverse communities tend to be more invasion resistant

(Crawley 1987, Burke and Grime 1996). This may occur because particular resident species or functional groups provide invasion resistance (Crawley et al. 1999, Levine and D'Antonio 1999, Symstad 2000, Hector et al. 2001, Dukes 2002, van Ruijven et al. 2003, Fargione and Tilman 2005) and these species or functional groups are more likely to be found in higher diversity communities. The importance of particular species for community invasion resistance is therefore analogous to a sampling effect in biodiversity–productivity relationships (Hector et al. 2001, Wardle 2001).

Finally, interactions between the invader and the invaded community might be key to understanding invasion success, analogous to a complementarity effect in biodiversity–productivity relationships (Hector et al. 2001, Fargione et al. 2003). In this case, not only the identity of the invader or the composition of the resident community, but the match between invaders and communities plus the respective species abundances would be most important in determining the outcome of invasion (e.g. Fargione et al. 2003, Turnbull et al. 2005b, Strauss et al. 2006). Thus, just like species coexistence in established communities, invasion and community re-assembly would be controlled by density-dependent stabilising mechanisms (Chesson 2000). These stabilising mechanisms would be expected to facilitate invasion by species or functional groups that are most different from abundant residents (MacArthur and Levins 1967, Abrams 1983, Emery 2007).

The most well-known and studied complementarity mechanism within temperate communities is based on resource-use niches (e.g. Harpole and Tilman 2007) which could lead to preferential invasion by species with complementary resource requirements compared with the residents (Fargione et al. 2003, Questad and Foster 2008). Increased invasion resistance of species-rich communities could, according to this hypothesis, be attributed to the lack of unconsumed resources, as some invasion studies have indicated (e.g. Knops et al. 1999, Hector et al. 2001, Fargione et al. 2003). Another stabilising mechanism potentially underlying invasion patterns is the presence of pathogens or herbivores – for which the invader is a host or resource – in a community that contains species closely-related to the invader. This mechanism is similar to the Janzen-Connell effect, in which the presence of adult trees reduces the recruitment success of conspecific juveniles in tropical forests (Janzen 1970, Connell 1971, Augspurger and Kelly 1984). We have previously found evidence for this mechanism, operating via negative soil feedbacks, in a temperate grassland community where it was a powerful promoter of coexistence between competing functional groups (Petermann et al. 2008). Hence, this pathogen-driven feedback could similarly affect invasion patterns and community re-assembly after invasion. Because functional groups are based on

species traits, taxonomy or both (for details regarding the functional group classification in this paper, see the Methods section), we expect species within functional groups to share more pests and pathogens (Gilbert and Webb 2007) and to have more similar resource requirements and resource-use patterns (Fargione et al. 2003). If invasion and community assembly are driven by one of these two stabilising mechanisms, between-functional group effects would be expected to be stronger than within-functional group effects.

In contrast to these deterministic explanations, invasion and community assembly could be independent of the biology of the species and instead be strongly influenced by chance (Hubbell and Foster 1986, Hubbell 2001). If invasion into new communities is viewed in the light of island biogeographic theory (MacArthur and Wilson 1963, 1967) the probability of colonisation by new species inevitably decreases with increasing species richness of the resident community because a larger fraction of the total species pool has already arrived and established. Thus, a negative relationship between community richness and the number of invading species would be expected. At the same time, the number of species going extinct is predicted to increase with increasing resident species richness, as, for the same area, population sizes are smaller in diverse communities. Equilibrium richness is reached when extinction and colonisation rates become equal. Under this neutral scenario, the compositions of the assembling communities would be random, meaning that they are not predictable based on the biology of the species, but instead governed only by demographic and dispersal stochasticity (Hubbell 2001). In the case of established communities of different initial richness and composition, invasion of new species and subsequent community re-assembly would then lead to the convergence of species richness but not of composition, even under identical environmental conditions (Fukami et al. 2005). This was indeed found by two recent studies examining spontaneous invasion via natural dispersal into experimental grassland communities of originally different richness levels and compositions (Pfisterer et al. 2004, Rixen et al. 2008). Species have often been shown to be limited by their dispersal abilities (Turnbull et al. 2000, Clark et al. 2007), and propagule pressure has been identified as a major driver of invasion and community assembly (e.g. Kolar and Lodge 2001). Thus, the compositional divergence of different communities observed in spontaneous invasion studies may well be due to dispersal stochasticity. On the other hand, initial floristic composition (Egler 1954, Collins et al. 1995) or the order of species arrivals (Drake 1990, Chase 2003, Zhang and Zhang 2007) may prevent compositional convergence. In this case, the communities` colonisation and establishment history may override all other assembly

mechanisms and may have a dominant influence on the final composition of re-assembled communities (Drake 1991).

The functioning of plant communities, for example in terms of primary productivity, has been found to be a function of species richness (Tilman et al. 1996, Hector et al. 1999, Tilman et al. 2001), phylogenetic diversity (Cadotte et al. 2008), functional richness (Tilman et al. 1997, Hector et al. 1999), evenness (Wilsey and Potvin 2000, Polley et al. 2003, Hillebrand et al. 2008) and composition (Hooper and Vitousek 1997, Tilman et al. 1997, Spehn et al. 2005, for further references see Balvanera et al. 2006). Therefore, if invasion leads to changes in these properties, it is expected to directly or indirectly influence community functioning (Chase 2003, Hooper et al. 2005). However, the consequences of invasion for the invaded communities, especially with regard to their functioning, are rarely considered (Pfisterer et al. 2004, Rixen et al. 2008).

In the present study, we use an established grassland biodiversity experiment with a species richness and functional group richness gradient maintained by weeding to study the re-assembly of communities by invasion and the resulting effects on ecosystem functioning. After opening communities with different initial compositions to spontaneous invasion and to invasion assisted by seed addition, we examine whether invasion and re-assembly processes are dominated by biological characteristics of residents or invaders, by the chance effects of dispersal or by the compositional history of the resident community. Furthermore, we assess the consequence of invasion, not only for richness and composition but also for the functioning of re-assembled communities in terms of primary productivity. We show that invasion is biologically predictable on a functional group basis and only weakly dependent on dispersal effects. Invasion complements species richness and functional composition and thus leads to the decay of positive species richness–productivity relationships. We suggest that the observed community re-assembly processes were driven by both resource complementarity and pathogen effects.

Methods

Experimental design

The present study was carried out within a large experimental platform at Jena, Germany (50° 55´ N, 11° 35´ E). The Jena Experiment is a long-term grassland biodiversity–ecosystem functioning experiment (Roscher et al. 2004). It is situated in the floodplain of the river Saale at an altitude of 130 m above sea level and until 2001 it was used for agricultural crops. The

experimental grassland plots were established by sowing in spring 2002. The mean annual air temperature is 9.3 °C, the mean annual precipitation is 587 mm.

Seventy-eight experimental plots were sown with randomly assembled species assemblages of one, two, four, eight or 16 species. The total species pool of the experiment consisted of 60 native central European plant species common in semi-natural grasslands. Four plots containing all 60 species were also sown. Prior to assembling experimental communities, the species were grouped into four functional groups according to a cluster analysis using ecological and morphological traits (16 grasses, 12 legumes, 12 small herbs, 20 tall herbs, Roscher et al. 2004). Each functional group was represented at each richness level. In addition, the number of functional groups was varied within species richness levels as much as possible, including 16-species richness levels with only one functional group, so that the design was almost completely orthogonal with respect to functional group composition and species richness (Roscher et al. 2004). There were 16 different species in monoculture, 16 different species compositions at richness levels 2, 4, and 8, and 14 different species compositions at richness level 16 (see Appendix C: Table C1). The plots had a size of 20 x 20 m and were arranged in four blocks. In addition, each plot was assigned x- and y-coordinates to account for geographical position in later analyses. All plots were mown twice a year and did not receive fertiliser.

Within each plot, we marked four 2 x 2.25 m subplots for our invasion experiment. One pair of subplots was used for the invasion treatment "cessation of weeding" (c) and one pair for the treatment "weeding" (w). In each subplot pair, one subplot was randomly assigned to the deliberate seed addition treatment (+) and the other received only spontaneous invader seeds (-). The seed addition treatment included seeds of all species from the original experimental pool of 60 species and we therefore refer to them as "internal invaders" if they are not part of the sown community of a specific plot. Seeds were added at a rate of 1000 viable (according to standard laboratory tests) seeds per m^2 in April 2005 divided equally among the 60 species. Among the spontaneously (= naturally) invading species there were both "internal invaders" and "external invaders", the latter not belonging to the original pool of 60 species but occurring in the surroundings of the field site. Thus, our experimental design consisted of the following four subplots: subplot "w-" was weeded twice a year like the remainder of the larger 20 x 20 m plot to maintain the original set of species ("residents") and served as the control ("closed" community). In subplot "w+" internal invader seeds were added and external invader species were removed by weeding, so that only internal invaders could establish. In subplot "c-" weeding was stopped at the end of 2004; hence, internal

invaders and external invaders could enter the community spontaneously. In subplot "c+" weeding was also stopped at the end of 2004, so that internal and external species could invade spontaneously; additionally, internal invader seeds were added. Generally, soil disturbance caused by weeding was kept to a minimum by using small knifes to cut weed roots and remove them carefully and by all maintenance being done before the development of a closed canopy (early April at the start of the growing season, and July after the first mowing).

We harvested aboveground plant biomass (above 3 cm) twice a year for 3 years after the start of the invasion experiment, i.e. from year 4–6 after the initial establishment of the plots. Harvests were timed to coincide with typical grassland harvest times in central Europe (late May and August). In each subplot we randomly selected an area of 20 x 50 cm for harvest. We sorted the harvested plant material into species, except in the first of the two harvests in 2005, when we only sorted into residents, internal invaders and external invaders and noted the number of species in each category. Harvested biomass was dried and weighed. Comparative data from weeded monocultures of all 60 species and weeded 60-species mixtures were available from another study within the Jena Experiment (Marquard et al. in press).

Data analysis

We analysed the biomass and the number of species of residents and internal and external invaders as a function of the design variables and covariates with ordinary mixed-model analyses of variance (Snedecor and Cochran 1980). Fixed and random terms were fitted sequentially by multiple regression and results summarized in analysis of variance (ANOVA) tables (for more details, see Schmid et al. 2002). Biomass (in gm^{-2}) was analysed as a yearly total, and species richness (per harvest quadrat) as an average of the two harvests per year. Because sown resident species richness in the plots was highly correlated with realised resident species richness in the harvested area at the start of our experiment, we used sown plot richness in all analyses that investigate the influence of pre-invasion community properties on invasion. Results did not change when realised richness was used. The number of internal invader species and their biomass was analysed on a functional group basis in a "home-away" contrast analysis. This allowed a test of the difference in invasion success between communities where each functional group occurred among the residents ("home") and where it did not ("away"). In the home-away biomass analysis we included only data

from 2006 and 2007, as the biomass of individual functional groups was only available for one of the two harvests in 2005.

The first section of this paper focuses on the influence of community properties and invader species characteristics on invasion success. Therefore, only data from invaded subplots were used (c-, c+ and w+) in the respective analyses. The second section of the paper deals with community changes in response to invasion. Thus, the development of the non-invaded subplot (w-) was compared with invaded subplots that contained the full invader range (external and internal invaders: c- and c+). All analyses that classify invaders by functional group exclude external invaders because the grouping of internal species into functional groups was based on an *a priori* cluster analysis (see section Experimental design above) and external invaders occurred in very low species numbers and abundance. Data were analysed using the statistical software R 2.7.2 (http://www.r-project.org) and GenStat (11th edition, VSN International, 2008). All error bars and errors accompanying mean values represent ±1 standard error of the mean.

Results

Community invasibility

Following the cessation of the weeding regime, communities of residents accumulated increasing numbers of invader species with time. However, the number and biomass of internal invader species (species that belonged to the species pool of the experiment) and external invader species decreased with increasing resident species richness, i.e. resistance to invasion increased with resident species richness (Fig. 1, $F_{1,63}$=80.23, P<0.001 for the number of internal invader species; $F_{1,63}$=32.03, P<0.001 for internal invader biomass; $F_{1,67}$=22.03, P<0.001 for the number of external invader species; $F_{1,67}$=13.61, P<0.001 for external invader biomass—full ANOVAs can be found in Tables C2–C4). For internal invaders, this effect may in part be due to the decrease in the number of potential internal invader species in more diverse plots (MacArthur and Wilson 1967, Hector et al. 2001). However, this cannot apply to external invaders because their number is not intrinsically related to the number of resident species. Because the biomass of the resident community increased with sown species richness, we tested its direct effect on invader success by including resident biomass as a covariate in the analysis. Resident biomass had a strong negative effect on the number and biomass of internal and external invader species ($F_{1,920}$=106.20, P<0.001 for the number of internal invader species; $F_{1,920}$=514.27, P<0.001 for internal invader biomass; $F_{1,160}$=79.32, P<0.001 for the number of external invader species; $F_{1,160}$=10.36, P=0.002 for external invader

biomass). Nevertheless, the inclusion of resident biomass as a covariate did not affect the significance of subsequent terms in the ANOVA, indicating that resident biomass effects were additive to the other effects.

Invasiveness

Internal invader species were much more successful than external invaders in invading new communities, even if their seeds were not added deliberately. On average, internal invaders made up 85% of all invader species and 95% of total invader biomass (Fig. 1). Compared with the spontaneous invasion treatment, the deliberate addition of seeds of internal invaders further increased the number of successfully invading internal species when resident species richness was low (Fig. 1a, $F_{1,596}$=47.44, P<0.001 for the interaction "Species richness x Seed addition") and increased internal invader biomass at all species richness levels (Fig. 1c, $F_{1,595}$=8.4, P=0.004 for the term "Seed addition"). External invaders were neither negatively nor positively affected by the experimental addition of seeds of internal species (Fig. 1b and d, $F_{1,75}$=2.47, P=0.120 for the number of external invader species; and $F_{1,75}$=0.80, P=0.375 for external invader biomass). Furthermore, there was no effect of external invaders on invasion success of internal invaders ($F_{1,155}$=0.25, P=0.620 for the number of external invader species; $F_{1,155}$=0.28, P=0.600 for external invader biomass).

Because of the small biomass contribution of external invaders further analyses were carried out only for internal invaders. Among internal invaders, functional groups and species still varied widely in their ability to establish in new communities. The most successful invading functional groups in terms of the number of established species were grasses and small herbs (1.2±0.01 and 1.1±0.01 invader species per harvest quadrat, vs. 0.6±0.01 legume and 0.6±0.01 tall herb invader species per quadrat). Grass and legume invaders produced the highest biomass (89±4 gm^{-2} and 87±4 gm^{-2}, vs. 57±4 gm^{-2} and 35±4 gm^{-2} for small herb and tall herb invaders, respectively). When all internal invaders were examined separately at the species level, we found that the invasiveness of a species in terms of biomass production in a new community was weakly positively correlated with its aboveground biomass in monoculture (R^2 =0.15, $F_{1,57}$ =10.14, P=0.002) but strongly positively correlated with its aboveground biomass in 60-species mixtures (R^2 =0.51, $F_{1,55}$=55.29, P<0.001). Thus, the best predictor of invader performance was resident performance of the particular species in highly diverse resident communities.

The success of invader species or functional groups also depended on the interaction between the invader and the resident species in a community. Both the number of internal

invader species and their biomass were reduced when the functional group they belonged to was already present among the residents ("home"), compared to when it was absent ("away", Fig. 2). We analysed this negative interaction (negative "home-away effect") between the same resident and invading functional groups as a separate contrast within all resident and invading functional group-interactions and found it to be significant ($F_{1,11}$=37.94, P<0.001 for species number; $F_{1,11}$=6.50, P=0.027 for biomass). Additional interactions between resident and invader functional groups also influenced invader success. However, these other interactions were less important than the negative home-away effect and the latter was even significant when tested against these other interactions (i.e. the deviation from main contrast). We found a stronger negative home-away effect with seed addition than with spontaneous invasion ($F_{1,11}$=20.41, P<0.001 for the number of species, $F_{1,11}$=6.65, P=0.026 for biomass).

Because we could not distinguish between invader and resident individuals of the same species, species-level home-away effects on invader biomass could not be measured. However, when negative home-away effects on invader biomass at the functional group level were examined separately for all species, it became apparent that about two thirds of the species experienced these negative home-away effects. They were strongest for species that were generally successful invaders (in terms of biomass production), while species with generally low invasiveness experienced neutral to positive home-away effects (Fig. 2c).

Community convergence through invasion

Species richness, functional richness and productivity

Following the cessation of weeding, total species richness of communities with initially low richness experienced a major richness increase while those communities with the highest original species richness showed a slight decrease in species richness, leading to convergence in species richness due to invasion (Fig. 3, $F_{1,224}$=20.98, P<0.001 for the interaction "Species richness (log_2) x Invasion x Year"—the full ANOVA can be found in Table C5). At the same time, the number of resident species in the weeded controls remained relatively constant. Seed addition caused the total species richness of the invaded communities to increase slightly more rapidly than in communities with spontaneous invasion ($F_{1,224}$=3.02, P=0.084 for the interaction "Species richness (log_2) x Seed addition x Year"), especially in communities with originally low resident species richness, and to reach somewhat higher levels at the end of the observation period ($F_{1,224}$=27.46, P<0.001 for the interaction "Seed addition x Year"). If the lines in Fig. 3a were extended beyond 2007, monocultures and 60-species mixtures were predicted to cross in 2009 at a richness level of 12 species (per harvest quadrat) with only

spontaneous invasion, whereas the lines for communities receiving deliberate seed additions (Fig. 3b) were predicted to cross in 2008 at a level of 15 species. This suggests that with the pressure of seed addition, species richness converges more rapidly. The number of resident species remained stable during the invasion phase in all plots except the 16 and 60-species mixtures, where slight decreases over time were observed (data for residents not shown separately). All increases in species richness were entirely due to newly establishing invader species and not to a re-invasion of previously extinct residents.

While species richness had not fully converged by the end of the experiment, functional richness increased rapidly in invaded communities and in the last year of observation, 69 and 77 out of 82 communities in the spontaneous invasion and seed addition treatments, respectively, contained all four functional groups, even in the rather small area that was harvested. In contrast, only 12 out of 82 control communities contained all four functional groups in an area of the same size. Shannon diversity indices for functional group richness remained low in weeded controls until the end of the observation period ($H=0.55\pm0.02$ if based on the relative number of species in each functional group and $H=0.41\pm0.02$ if based on the relative biomass in each functional group) but increased in spontaneous invasion ($H=1.22\pm0.02$ if based on the number of species and $H=0.94\pm0.02$ if based on biomass) and seed addition treatments ($H=1.30\pm0.02$ if based on the number of species and $H=1.06\pm0.02$ if based on biomass). Not only did invasion lead to high functional group richness but also to the convergence of functional group proportions to similar levels in previously different communities (Figs. 4 and B1). The average composition of the biomass in invaded subplots at the end of the experiment was 30% grasses, 29% legumes, 24% small herbs and 17% tall herbs, and thus showed very high functional evenness.

Community biomass was much more variable than species richness and functional richness, and this was largely due to the biomass of resident species varying between years. The biomass of invaders increased over the course of the experiment ($F_{1,921}=154.69$, $P<0.001$), except in the 60-species mixtures, where it remained close to zero. In general, total community biomass increased from 2005 to 2007 in invaded communities ($F_{1,224}=16.54$, $P<0.001$ for the interaction "Invasion x Year"), but increased most strongly in communities with originally low resident species richness. Therefore, communities of different levels of original species richness and hence different community biomass production became more similar following invasion ($F_{1,150}=14.99$ $P<0.001$ for the interaction "Species richness (log2) x Invasion").

Biodiversity–productivity relationship

At the beginning of the experiment in 2005, we found a positive realised species richness–productivity relationship in all subplots (Fig. 5a). This relationship was maintained across the 3 years in the weeded control subplots (grey lines in Fig. 5). However, in the subplots which were opened to invasion, the positive relationship decayed over time (black lines in Fig. 5, Table C6, $F_{1,239}$=5.80, P=0.017 for the interaction "Realised richness (log2) x Invasion x Year"). This decay occurred more rapidly in subplots with deliberate seed addition than in subplots with only spontaneous invasion: the positive relationship had disappeared by 2006 in subplots where invasion was assisted by seed addition, and by 2007 in subplots with spontaneous invasion (Fig. 5).

In contrast to the species richness–productivity relationship, the relationships between the proportion of particular functional groups (based on their realised biomass) and community productivity did not decay due to invasion but rather strengthened (Fig. 6, Table C7). Thus, invaded communities with an above-average proportion of legumes had above-average productivity; and invaded communities with an above-average proportion of small herbs had below-average productivity. The most productive invaded plots (Fig. 6 b and c) were originally mainly grass and small herb monocultures (e.g. *Poa pratensis*, *Festuca pratensis*, *Bellis perennis*, *Plantago lanceolata)* or non-legume mixtures (e.g. a *Plantago media*/*Taraxacum officinale* mixture, and a four-species tall herb mixture) and had obtained their high, probably unstable, legume proportions via invasion. In contrast, the least productive invaded plots (Fig. 6 e and f) were those where small herbs had been present in high proportions from the beginning and had not yet been reduced to the average level of around 24%. Most of these small herb-dominated communities contained *Prunella vulgaris* and *Ajuga reptans*, two small herb species that can form dense ground cover and can thus slow down invasion by other functional groups. Among the non-invaded communities, plots with 0% or 100% legumes were less productive than others, and plots with 0% small herbs were slightly less productive than those with a small proportion of small herbs.

Discussion

Invasibility and invasiveness

Our experiment confirms previous findings, that experimental communities with higher numbers of resident species are more resistant to invasion from both internal and external invaders than species-poor communities (Tilman 1997, Knops et al. 1999, Joshi et al. 2000, Levine 2000, Naeem et al. 2000, Hector et al. 2001, Kennedy et al. 2002, Fargione et al. 2003,

van Ruijven et al. 2003, Pfisterer et al. 2004, Maron and Marler 2008, Roscher et al. 2009a). We also found that the invasion process was highly non-random on the functional group level. Invasion success was partly related to the identity of the invader and to the presence of particular functional groups (e.g. legumes) in the resident community. However, invasion success was most strongly dependent on the biological difference between the invader and the invaded community (Strauss et al. 2006, Suter et al. 2007), permitting species that belonged to a functional group absent from a community to invade more easily than species belonging to a functional group already present (Fargione et al. 2003, Turnbull et al. 2005b, Mwangi et al. 2007). This strong negative interaction between residents and invaders of the same functional group could be due to overlapping resource requirements (e.g. Knops et al. 1999, Naeem et al. 2000, Fargione et al. 2003, Mwangi et al. 2007) or to the presence of natural enemies (Petermann et al. 2008). We discuss these possibilities in more detail in the next section. However, that the strongest invader species in our study were most strongly inhibited by this negative effect (see Fig. 2c) is supportive of its important role as a stabilising force in community assembly (Chesson 2000, Chave 2004).

Effects of invasion on community properties and functioning

After our experimental communities were opened to invasion, initially species-poor communities were supplemented with high numbers of invader species. In contrast, originally species-rich communities tended to lose resident species and our experimental communities converged towards species richness levels very similar to natural grasslands adjacent to our study plots (15–19 species per harvest quadrat). This suggests a shift of the experimentally-assembled communities toward naturally-assembled communities, at least in terms of species richness, and supports similar findings from invaded grasslands by Pfisterer et al. (2004) and Rixen et al. (2008). However, their studies lacked a weeded control and a seed addition treatment, and did not analyse whether invaders entered the community in a random or deterministic way. Both studies observed very little compositional convergence suggesting that stochastic effects strongly influenced the re-assembly of their communities (but perhaps the short observation time (Pfisterer et al. 2004) or slow plant growth in an alpine habitat (Rixen et al. 2008) also had an influence). In contrast, in the present study, non-random invasion led to a rapid convergence of functional group composition among plots and resulted in a high functional richness and evenness of most invaded communities by the end of the experiment. Our experimental communities apparently re-assembled toward a common community structure determined by site conditions. As a consequence of this re-assembly, the

communities lost their positive species richness–productivity relationship as indicated by previous experiments (Pfisterer et al. 2004, Rixen et al. 2008, Roscher et al. 2009b). Interestingly, observational biodiversity–ecosystem functioning studies within single sites similarly do not find positive species richness–productivity relationships. Thus, our results from re-assembled experimental communities help to reconcile apparently contrasting experimental and observational findings (Schmid and Hector 2004, Hector et al. 2007).

In contrast to the rapid decay of the positive species richness–productivity relationship, relationships between functional group proportions and productivity were maintained or even strengthened in invaded communities. More specifically, invaded communities with a high proportion of legumes produced more biomass, and even out-performed non-invaded communities containing only legumes (for a detailed analysis of functional group contributions to productivity in non-invaded communities of the Jena Experiment see Marquard et al. in press). In contrast, invaded (and non-invaded) communities with a high proportion of small herbs produced less biomass than other communities. Some of these unproductive small herb communities proved to be rather resistant to invasion, potentially due to a dense ground cover, representing a historical effect on community structure (Drake 1991). We know from another experiment within the same site that the manual removal of these unproductive species leads to a rapid increase in community biomass even with a loss of species richness (Schmitz 2007).

While invasion by legumes was beneficial for community productivity, communities which initially contained only legumes were not those with a high proportion of legumes after invasion, indicating that high legume proportions in these communities are not sustainable in the longer term and easily invaded in spite of their high productivity. Indeed, the invasion of legume-only communities by other functional groups sometimes led to decreased productivity of the resulting communities. It could be argued that if non-random invasion was mainly due to resource complementarity it should lead to increased community productivity because of the use of otherwise unconsumed resources by the invader. This argument is valid except for the rather unlikely case that invaders enter the community based on available resources but then "waste" resources, decreasing community productivity due to their inefficiency. In the case of legumes, unilateral facilitation, i.e. the enhancement of other functional groups by legumes due to their nitrogen-fixing ability (Temperton et al. 2007), would be another explanation for the invasibility by less productive functional groups. It is more likely, however, that pathogen-driven negative feedbacks promoted the non-random invasion of all functional groups into plots where pathogens of that specific functional group had not yet

accumulated; in other words where their pathogen-free niche was vacant (Turnbull et al. 2005b, Mwangi et al. 2007, Petermann et al. 2008). For legumes in particular, this mechanism is supported by reports on the general instability of experimental legume monocultures which often suffer from extensive pathogen attack (Pfisterer et al. 2004).

The influence of dispersal limitation

Our seed addition treatment was intended to reduce the influence of dispersal stochasticity on invasion and community convergence. Indeed, we found that the number of invader species, and, to a smaller extent, invader biomass, was lower in the spontaneous invasion treatment without experimental seed input. This indicates that even those species that were already present at the site were dispersal-limited (Roscher et al. 2009a). Under neutrality, dispersal limitation and the resulting stochasticity in colonisation rates are key factors shaping communities (Hubbell 2001, Chase 2003, Chase 2007). With dispersal limitation we would expect a greater stochastic and a smaller deterministic component in the re-assembly process (Chase 2007). This was exactly what we found: the deterministic control by functional groups was weaker in plots exposed only to spontaneous seed arrivals and the convergence process slower than when seeds were experimentally added. However, invasion into plots with only spontaneous dispersal was still deterministic on a functional group basis and led to analogous community convergence in terms of species richness, functional richness and productivity and to a decay of the species richness–productivity relationship. This supports our conclusion that the deterministic, biological component of community assembly was more important than chance in shaping post-assembly communities, at least in terms of their functional structure. While our experiment was not designed to test species-level determinism, we hypothesise that the non-random assembly mechanisms we observed may still operate among species within functional groups, even if in a less stringent way than among species between functional groups.

By following randomly-assembled communities of different species and functional composition for three years after opening them to spontaneous and assisted invasion we have shown that invasion success is strongly controlled by the richness of the community and operates in a biologically predictable way, at least on the functional group level. Specifically, invasion enhances low species richness and re-balances functional group composition. Consequently, communities with different richness and compositional histories converge at nearly maximum functional richness and evenness, regardless of dispersal limitation, rejecting purely neutral concepts of community assembly. Furthermore, we have shown that the

invasion process can lead to reduced productivity because communities of high productivity are not necessarily stable. This suggests a role for pathogens as drivers of community assembly, rather than a full control of floristic compositions by different resource requirements of species. We believe that our results and other work on invasion and assembly within native communities not only contribute to the fundamental understanding of how communities are structured and function, but can also help to direct restoration efforts (Temperton et al. 2004, Funk et al. 2008) and understand, predict and control non-native invasions (Shea and Chesson 2002, Funk et al. 2008).

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Figures

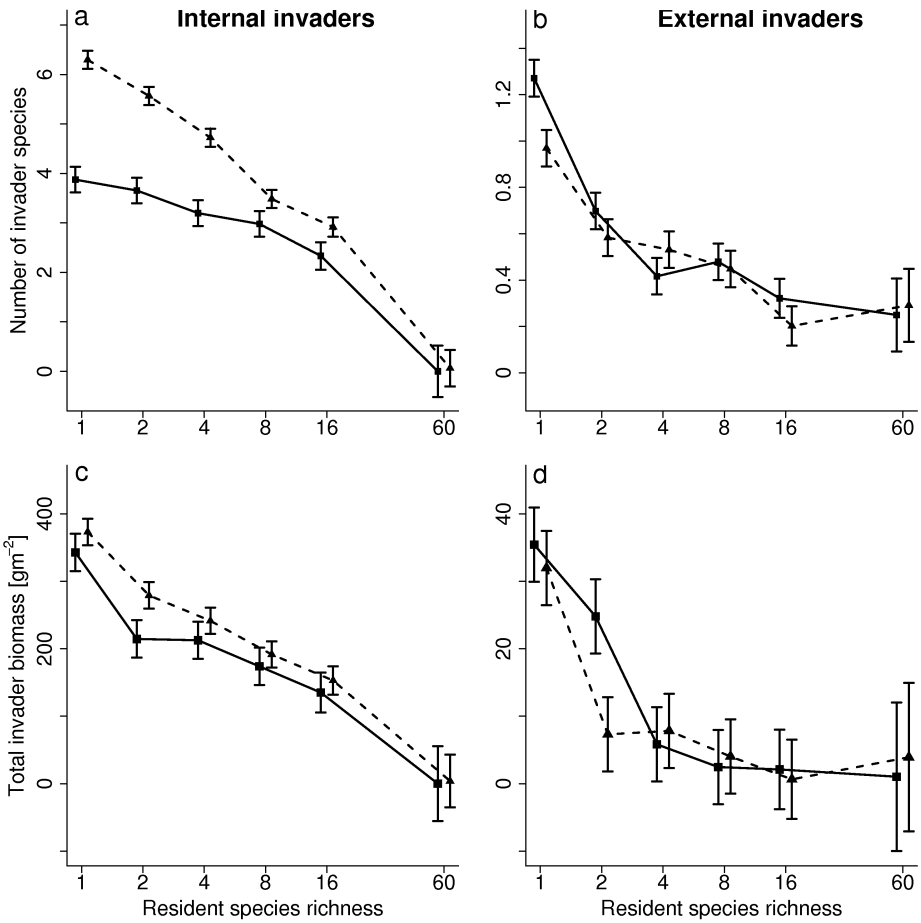

Fig. 1: The number of species (a, b) and the biomass (c, d) of internal and external invaders as a function of resident species richness. The solid lines represent subplots without seed addition, the dashed lines represent subplots with seed addition (see Methods section for details). The data were averaged over the six harvests from years 2005-2007. Note the change in the y-axis scale for the internal and external invaders. For statistical analysis, see Table C2.

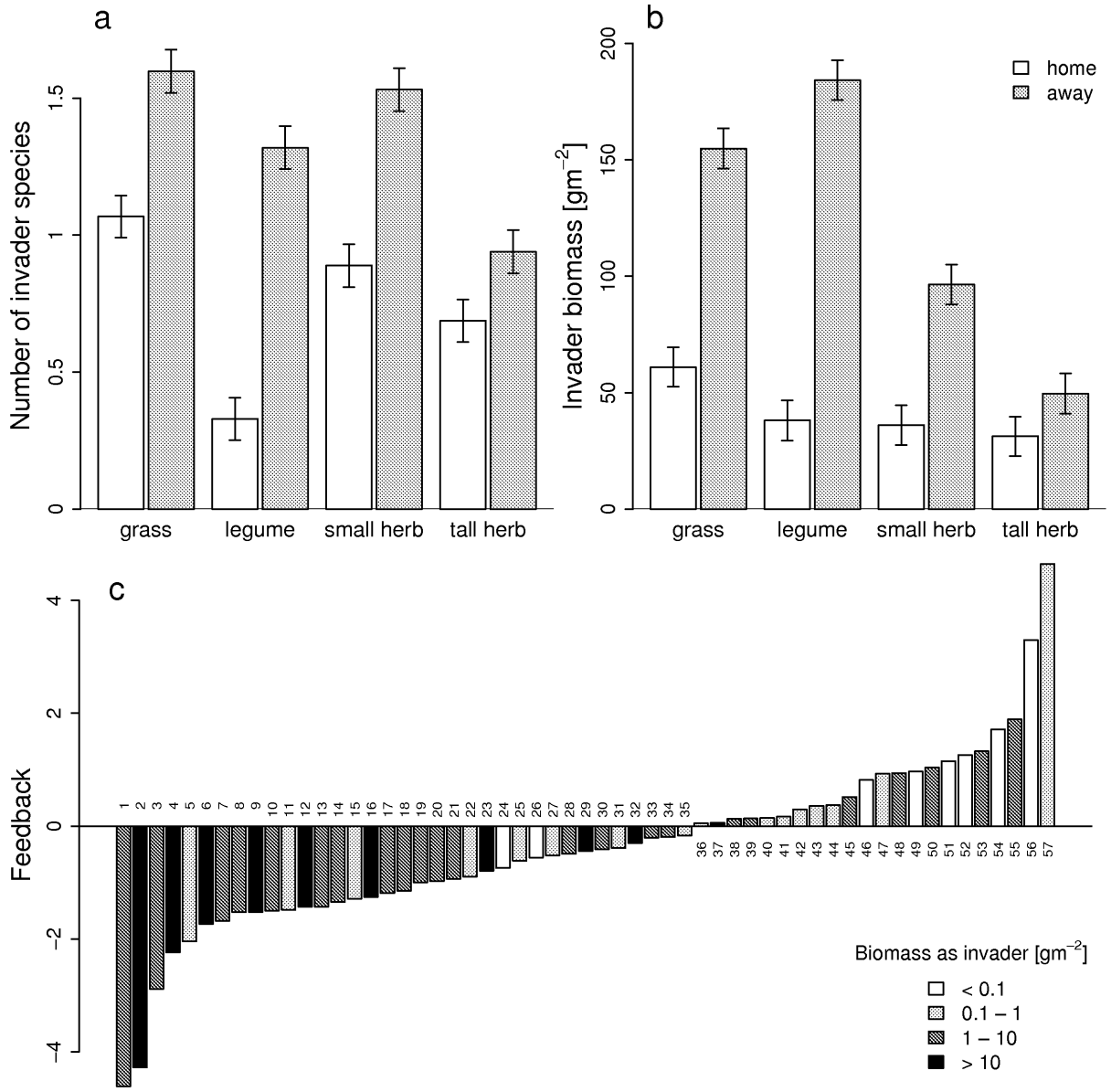

Fig. 2: Negative home-away effect when plants invade communities where their functional group is already present. The number of internal invader species (a) and the internal invader biomass (b) is shown separated into functional groups, with paired bars representing plots where the same functional group is already present with at least one species (white bars, "home") or where the same functional group is not yet present (grey bars, "away"). (c) Log-ratio of the home and away biomass of the internal invaders (log (biomass at home/ biomass away)). Negative log-ratio values correspond to a disadvantage in a home plot (negative "home-away effect"), positive log-ratio values indicate a home plot advantage (positive "home-away effect"). The effect is based on functional group–home and –away invasion, but each bar represents a single internal invader species (for species names see Appendix A1). All of the dominant invader species (black bars indicating average biomass in home and away communities >10gm^{-2}) experience negative home-away effects, whereas

subordinate species (white bars indicating average biomass in home and away communities <0.1gm^{-2}) show mostly positive home-away effects. The data were averaged across the three subplots (across the spontaneous invasion (treatment c-) and seed addition treatments (c+ and w+)), across 4 harvests from 2006-2007, and across species richness levels ranging from 1-16. For statistical analysis, see Table C2.

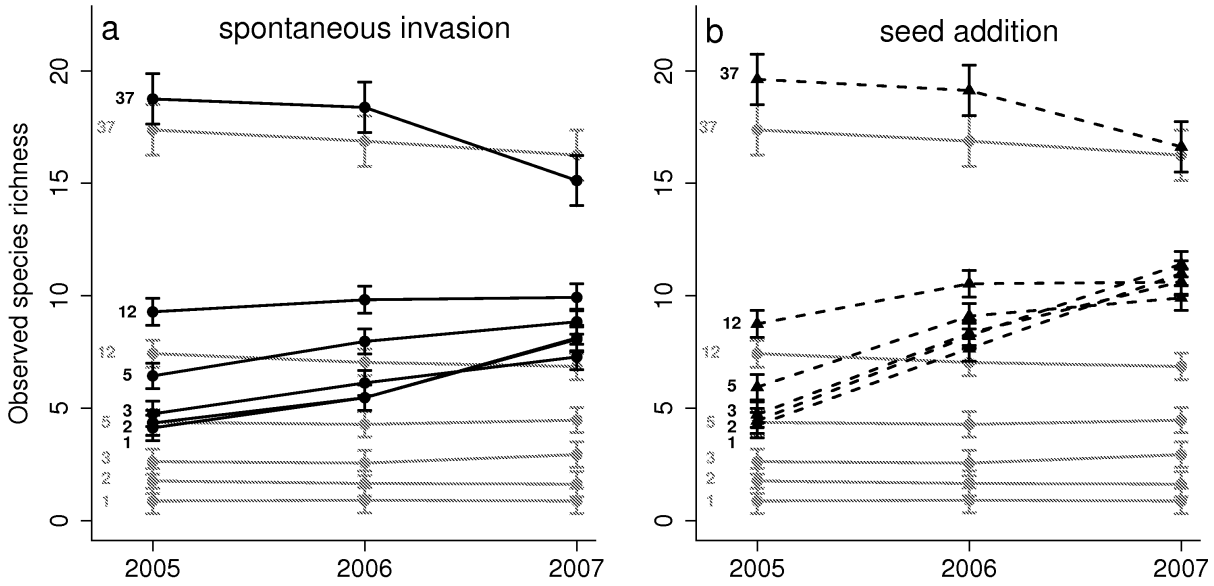

Fig. 3: Convergence of species richness in invaded communities. Note that species richness in weeded controls (grey lines) could only decline because all invaders were weeded out and were therefore not included in harvests. The species richness of invaded communities (black lines) includes residents and invaders (black solid lines in a: spontaneous invasion (c-) and black dashed lines in b: seed addition (c+)). The numbers at the beginning of each line depict the average species richness per 20 x 50cm harvest quadrat of the respective communities in 2003, prior to the start of the invasion experiment. For statistical analysis, see Table C5.

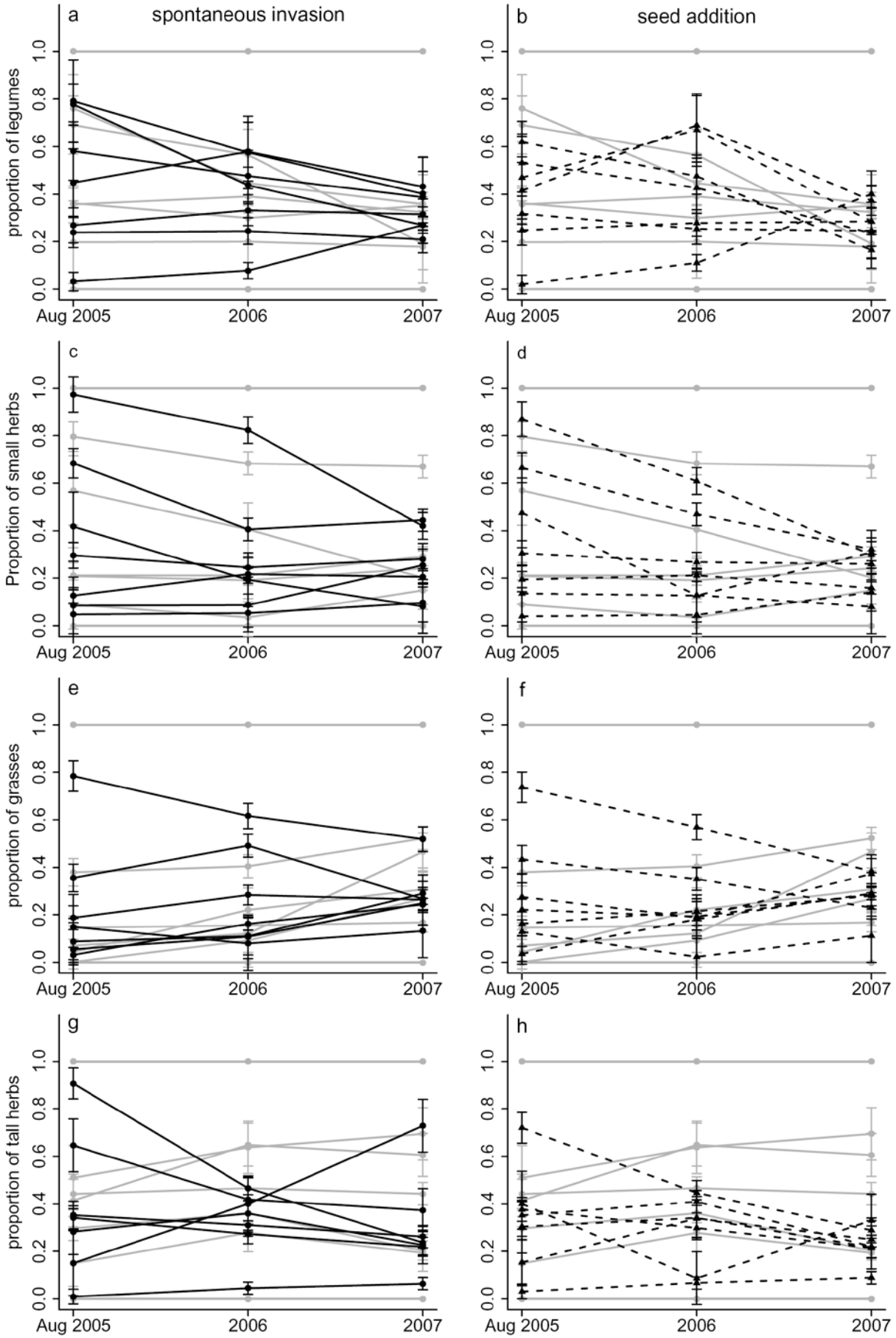
a
spontaneous invasion
b
seed addition
proportion of legumes
c
d
Proportion of small herbs
e
f
proportion of grasses
g
h
proportion of tall herbs
0.0
0.2
0.4
0.6
0.8
1.0
Aug 2005
2006
2007

Fig. 4: Convergence of the proportion of biomass accounted for by the four functional groups. Observed (=realised) proportions were calculated as observed biomass of the respective functional group per observed total target biomass. Here, external invaders were excluded because they could not be grouped into the same four functional groups, so target species in this case were residents in weeded controls (grey lines, w-), but residents and internal invaders in non-weeded subplots (black lines in the left column: spontaneous invasion c-, black dashed lines in the right column: seed addition c+). Legumes and small herbs were originally sown in the following proportions in 2002: 0, 0.2, 0.25, 0.3125, 0.375, 0.5 and 1, tall herbs: 0, 0.25, 0.3125, 0.333, 0.375, 0.5 and 1 and grasses: 0, 0.25, 0.267, 0.3125, 0.375, 0.5 and 1.

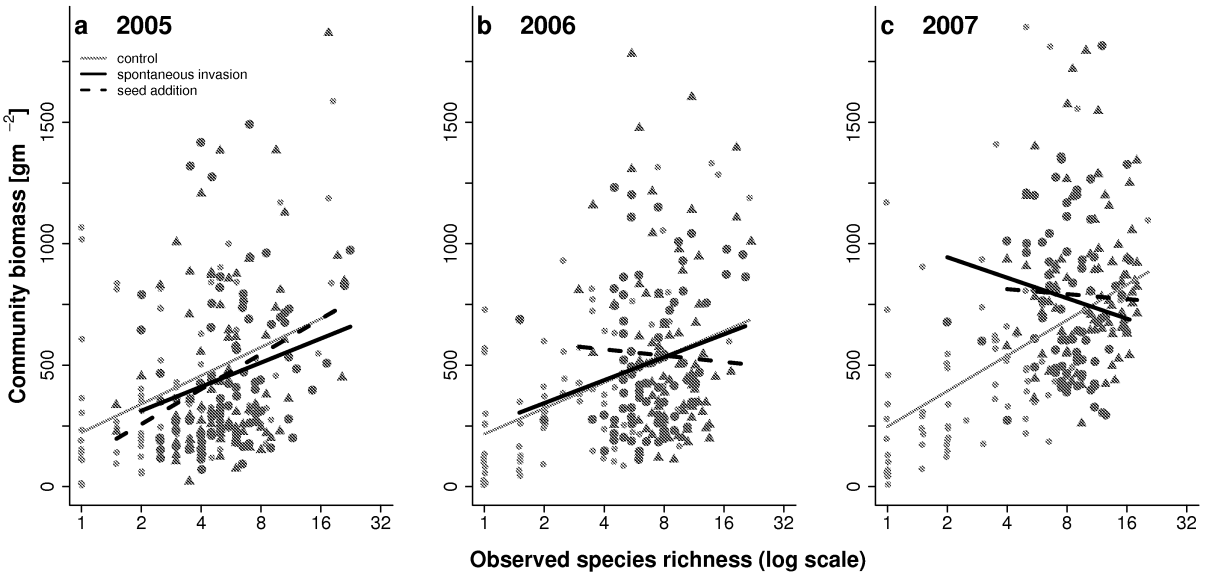

Fig. 5: Observed (=realised) species richness-productivity relationships over the course of three years. The light grey line and circles depict the weeded control (no invaders, treatment w-), the solid black line and dark grey circles depict the spontaneous invasion treatment (c-), the dashed line and dark grey triangles depict the seed addition treatment (c+). Note that regression lines are drawn only across the range of observed species richness values occurring in that respective treatment (one single outlier in 2006 and two in 2007, all three with very high biomass, are not shown). For statistical analysis, see Table C6.

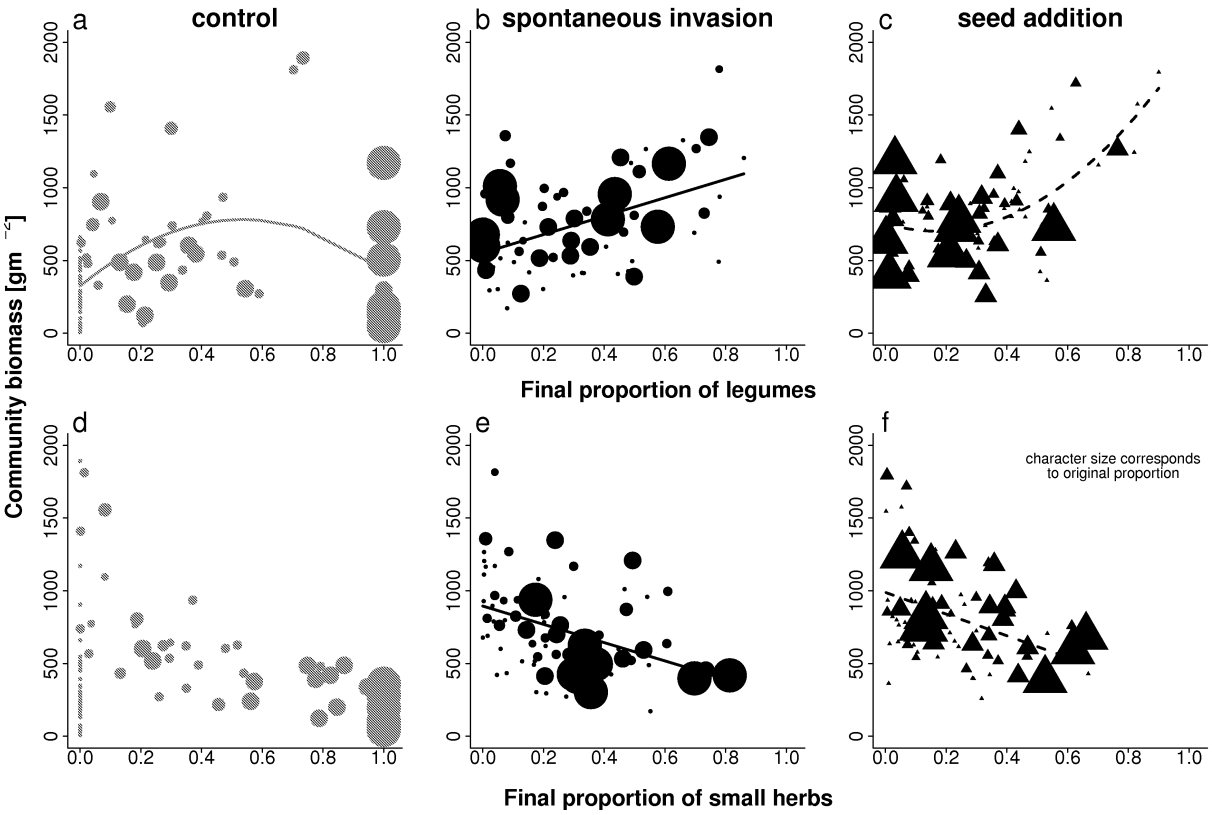

Fig. 6: Legume proportion-productivity relationships and small herb proportion-productivity relationships in the final year of the experiment. a and d: control (w-), b and e: spontaneous invasion (c-), c and f: seed addition (c+). Plotting character size is proportional to the original proportion of the respective functional group in the plot. Note that fitted lines are drawn only when the relationship is significant at $P<0.05$ and only across the range of realised proportion values occurring in that respective treatment (three outliers with very high biomass were excluded). For statistical analysis, see Table C7.

Appendix A

Appendix A1: List of internal invader species with corresponding numbers as in Fig. 2c. 1: *Trifolium hybridum*, 2: *Onobrychis viciifolia*, 3: *Lotus corniculatus*, 4: *Vicia angustifolia*, 5: *Lathyrus pratensis*, 6: *Dactylis glomerata*, 7: *Medicago lupulina*, 8: *Vicia cracca*, 9: *Trifolium pratense*, 10: *Festuca pratensis*, 11: *Ranunculus acris*, 12: *Trifolium repens*, 13: *Alopecurus pratensis*, 14: *Trifolium dubium*, 15: *Phleum pratense*, 16: *Poa trivialis*, 17: *Bromus hordeaceus*, 18: *Prunella vulgaris*, 19: *Crepis biennis*, 20: *Trifolium campestre*, 21: *Centaurea jacea*, 22: *Festuca rubra*, 23: *Arrhenatherum elatius*, 24: *Campanula patula*, 25: *Poa pratensis*, 26: *Primula veris*, 27: *Cirsium oleraceum*, 28: *Knautia arvensis*, 29: *Taraxacum officinale*, 30: *Plantago media*, 31: *Veronica chamaedrys*, 32: *Plantago lanceolata*, 33: *Galium mollugo*, 34: *Tragopogon pratensis*, 35: *Rumex acetosa*, 36: *Anthriscus sylvestris*, 37: *Leucanthemum vulgare*, 38: *Achillea millefolium*, 39: *Avenula pubescens*, 40: *Pimpinella major*, 41: *Geranium pratense*, 42: *Pastinaca sativa*, 43: *Leontodon hispidus*, 44: *Trifolium fragiferum*, 45: *Medicago varia*, 46: *Ranunculus repens*, 47: *Leontodon autumnalis*, 48: *Trisetum flavescens*, 49: *Glechoma hederacea*, 50: *Daucus carota*, 51: *Bellis perenne*, 52: *Ajuga reptans*, 53: *Bromus erectus*, 54: *Anthoxanthum odoratum*, 55: *Holcus lanatus*, 56: *Cardamine pratensis*, 57: *Carum carvi*. The following species are missing from the graph because their average biomass as invaders at home or away was zero and hence no home-away effect could be calculated: *Luzula campestris*, *Cynosurus cristatus*, *Heracleum sphondylium*, *Sanguisorba officinalis*. The external species *Vicia angustifoila* (number 4) was accidentally sown as an internal invader into all subplots with seed addition and therefore treated as an internal invader in all analyses. Nomenclature follows Rothmaler (2002).

Appendix B

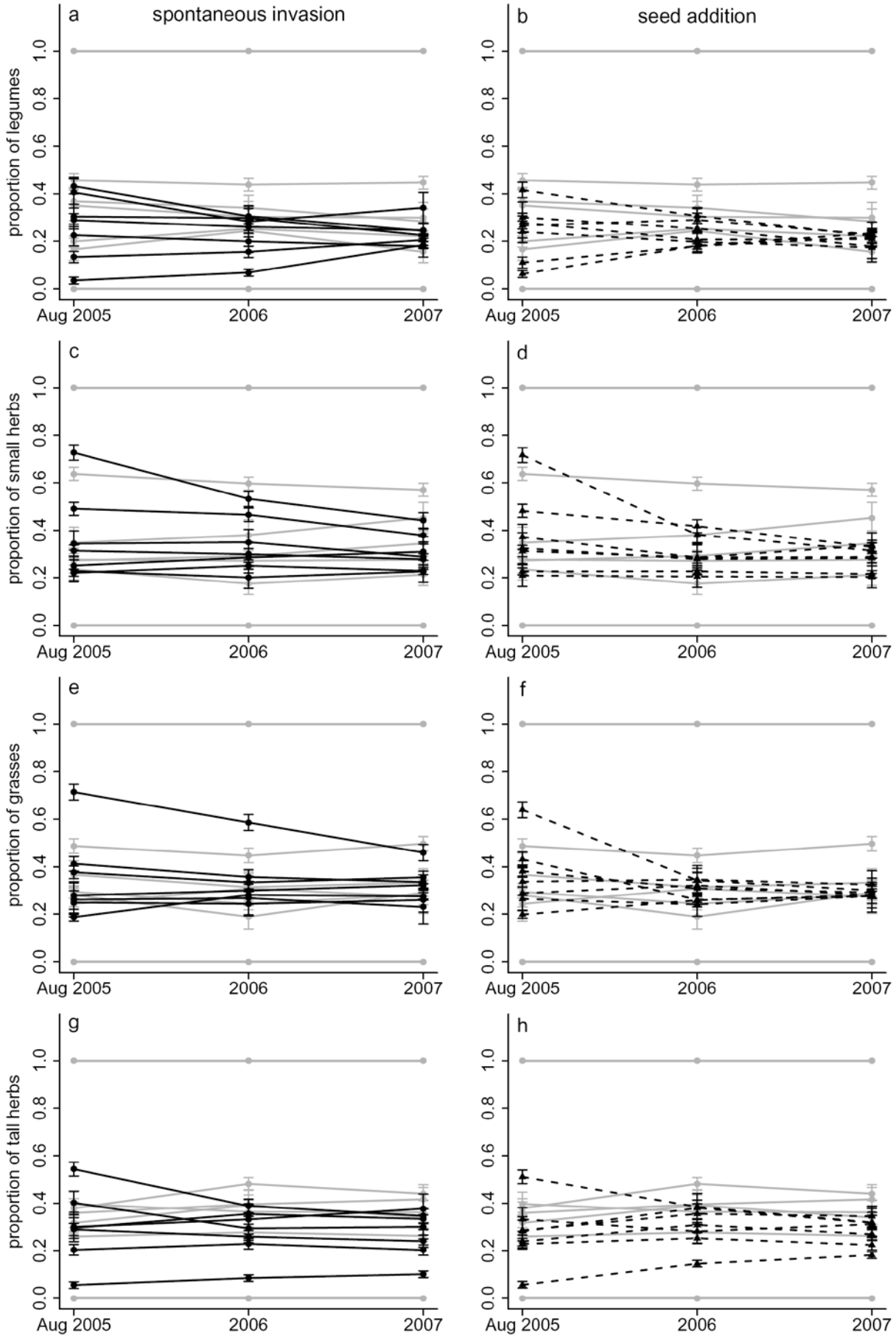
a
spontaneous invasion
b
seed addition
c
d
e
f
g
h
proportion of legumes
proportion of small herbs
proportion of grasses
proportion of tall herbs
0.0
0.2
0.4
0.6
0.8
1.0
Aug 2005
2006
2007

Fig. B1: Convergence of the proportion of the total number of species accounted for by the four functional groups. Observed (=realised) proportions were calculated as observed number of species of the respective functional group per observed number of total target species. Here, external invaders were excluded because they could not be grouped into the same four functional groups, so target species in this case were residents in weeded controls (grey lines, w-), but residents and internal invaders in non-weeded subplots (black lines in the left column: spontaneous invasion c-, black dashed lines in the right column: seed addition c+). Small herbs and legumes were originally sown in the following proportions in 2002: 0, 0.2, 0.25, 0.3125, 0.375, 0.5 and 1, tall herbs: 0, 0.25, 0.3125, 0.333, 0.375, 0.5 and 1 and grasses: 0, 0.25, 0.267, 0.3125, 0.375, 0.5 and 1.

Appendix C

Table C1: Experimental design. Original (sown) species richness and functional group composition of resident communities in the Jena Experiment.

Species richness	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**
grasses	1				2				1		1		4				2		2		2	1	1		1
small herbs		1				2			1			1		4			2			2	1		1	2	1
tall herbs			1				2			1	1				4			2	2		1	2		1	1
legumes				1				2		1		1				4		2		2		1	2	1	1
Replicates	4	4	4	4	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	4

Species richness	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**16**	**16**	**16**	**16**	**16**	**16**	**16**	**16**	**16**	**16**	**60**
grasses	8				4		4		2	3	3		2	16		8		8		5	5	6		4	16
small herbs		8			4			4	3		3	2	2			8			8	6		5	6	4	12
tall herbs			8			4	4		3	2		3	2		16		8	8		6	5		5	4	20
legumes				8		4		4		3	2	3	2				8		8		6	5	5	4	12
Replicates	1	1	1	1	1	1	1	1	1	1	1	1	4	1	1	1	1	1	1	1	1	1	1	4	4

Table C2: Analysis of variance (ANOVA) of the number of species and the biomass (gm^{-2}) of internal invaders per functional group per harvest quadrat. Data exclude the 60-species level, because it always contains all four functional groups. The inclusion of resident biomass as a covariable did not change the significance of the results and was omitted from the model. "Species richness" stands for the log_2-transformed sown species richness of the resident community. The deviation of the species richness effect from log-linearity was not significant and omitted. The results were relatively robust to the order of the terms species richness and presence of particular functional groups, so only the results from the model with species richness tested first are shown. The presence of the four functional groups was tested in the order of their explanatory power in the model. Two- and three-way interactions of functional group effects were small and therefore omitted from the model. The weeding and seed addition treatments (c-, c+ and w+) were used to form two contrasts. Only the first of them ("Seed addition"), representing seed addition (c+ and w+) vs. no seed addition treatments (c-), was included in the model (the contrast between w+ and c+ was not significant). The "Home-away contrast", which represents the main contrast within the total "Invader x resident FG" interactions was tested against its deviation ("Other invader-resident FG interactions"). Other error terms are printed in italics. FG = functional group.

	Number of species				Biomass			
Source	**df**	**SS**	**F**	**P**	**df**	**SS**	**F**	**P**
Spatial variation	9	51.1	3.01	0.005	9	619241	2.70	0.010
Species richness	1	151.3	80.23	<0.001	1	815930	32.03	<0.001
Legume presence	1	83.7	44.38	<0.001	1	302853	11.89	0.001
Tall herb presence	1	18.7	9.89	0.003	1	85362	3.35	0.072
Grass presence	1	0.1	0.05	0.827	1	31173	1.22	0.273
Small herb presence	1	0.2	0.09	0.771	1	8594	0.34	0.563
Plot	*63*	*118.8*	*1.57*	*0.010*	*63*	*1604762*	*0.75*	*0.907*
Invader FG	3	154.1	42.67	<0.001	3	1602127	15.77	<0.001
Home-away contrast	1	145.8	37.94	<0.001	1	2071215	6.50	0.027
Other invader-resident FG interactions	11	42.3	3.19	<0.001	11	3506087	9.41	<0.001
Species richness x Home-away contrast	1	4.5	1.77	0.205	1	15375	0.14	0.710
Species richness x Other invader-resident FG interactions	14	35.2	2.09	0.014	14	1493090	3.15	<0.001
Plot x Invader FG	*201*	*242.0*	*2.88*	*<0.001*	*202*	*6841052*	*3.03*	*<0.001*
Seed addition	1	75.4	180.62	<0.001	1	93776	8.40	0.004
Species richness x Seed addition	1	19.8	47.44	<0.001	1	15019	1.35	0.246
Legume presence x Seed addition	1	19.6	46.91	<0.001	1	3215	0.29	0.591
Tall herb presence x Seed addition	1	1.1	2.66	0.104	1	1568	0.14	0.708
Grass presence x Seed addition	1	0.1	0.20	0.652	1	15890	1.42	0.233
Small herb presence x Seed addition	1	0.0	0.09	0.770	1	62645	5.61	0.018
Invader FG x Seed addition	3	13.9	11.07	<0.001	3	181883	5.43	<0.001
Home-away contrast x Seed addition	1	13.6	20.41	<0.001	1	119186	6.65	0.026
Other invader-resident FG interactions x Seed addition	11	7.3	1.59	0.097	11	197138	1.61	0.093
Plot x Invader FG x Subplot	*596*	*248.8*	*0.57*	*1.000*	*595*	*6639929*	*0.75*	*1.000*
Year	1	580.2	791.58	<0.001	1	2289985	154.69	<0.001
Plot x Invader FG x Subplot x Year	*901*	*660.4*	*2.49*	*<0.001*				
Residual	*944*	*278.3*			*921*	*13634455*	*0.65*	*1.000*

Table C3: Analysis of variance (ANOVA) of the number of species of external invaders per harvest quadrat. Data exclude the 60-species level. The inclusion of resident biomass as a covariable did not change the significance of the results and was omitted from the model. "Species richness" stands for the log_2-transformed sown species richness of the resident community. The deviation of the species richness effect from log-linearity was not significant and omitted. The results were relatively robust to the order of the terms species richness and presence of particular functional groups, so only the results from the model with species richness tested first are shown. The presence of the four functional groups was tested in the order of their explanatory power in the model. Two- and three-way interactions of functional group effects were small and therefore omitted from the model. All error terms are printed in italics.

	df	**SS**	**F**	**P**
Spatial variation	9	10.3663	0.88	0.549
Species richness	1	28.9082	22.03	<0.001
Legume presence	1	10.9671	8.36	0.005
Small herb presence	1	6.0697	4.63	0.035
Tall herb presence	1	0.0013	0.00	0.975
Grass presence	1	0.2808	0.21	0.645
Plot	*67*	*87.9229*	*4.12*	*<0.001*
Seed addition	1	0.823	2.58	0.112
Species richness x Seed addition	1	0.6031	1.89	0.173
Legume presence x Seed addition	1	0.0001	0.00	0.986
Small herb presence x Seed addition	1	1.2136	3.81	0.055
Tall herb presence x Seed addition	1	0.7482	2.35	0.130
Grass presence x Seed addition	1	0.044	0.14	0.711
Plot x Subplot	*76*	*24.2346*	*1.18*	*0.190*
Year	1	2.686	9.97	0.002
Species richness x Year	1	1.0648	3.95	0.049
Legume presence x Year	1	2.732	10.14	0.002
Small herb presence x Year	1	2.3659	8.78	0.004
Tall herb presence x Year	1	0.0043	0.02	0.900
Grass presence x Year	1	0.3525	1.31	0.255
Seed addition x Year	1	0.1736	0.64	0.423
Plot x Subplot Year	*155*	*41.7673*	*0.91*	*0.713*
Residual	*160*	*47.1871*		

Table C4: Analysis of variance (ANOVA) of the biomass (gm^{-2}) of external invaders per harvest quadrat. Data exclude the 60-species level. The inclusion of resident biomass as a covariable did not change the significance of the results and was omitted from the model. "Species richness" stands for the log_2-transformed sown species richness of the resident community. The deviation of the species richness effect from log-linearity was not significant and omitted. The results were relatively robust to the order of the terms species richness and presence of particular functional groups, so only the results from the model with species richness tested first are shown. The presence of the four functional groups was tested in the order of their explanatory power in the model. Two- and three-way interactions of functional group effects were small and therefore omitted from the model. All error terms are printed in italics.

	df	**SS**	**F**	**P**
Spatial variation	9	42165	1.66	0.115
Species richness	1	38314	13.61	<0.001
Grass presence	1	4248	1.51	0.224
Small herb presence	1	3561	1.26	0.265
Legume presence	1	4541	1.61	0.209
Tall herb presence	1	0	0.00	1.000
Plot	*67*	*188639*	*1.58*	*0.027*
Seed addition	1	1522	0.85	0.359
Species richness x Seed addition	1	1535	0.86	0.357
Grass presence x Seed addition	1	31	0.02	0.896
Small herb presence x Seed addition	1	570	0.32	0.574
Legume presence x Seed addition	1	763	0.43	0.515
Tall herb presence x Seed addition	1	4455	2.49	0.118
Plot x Subplot	*76*	*135726*	*2.61*	*<0.001*
Year	1	5827	8.53	0.004
Species richness x Year	1	3751	5.49	0.020
Grass presence x Year	1	230	0.34	0.563
Small herb presence x Year	1	634	0.93	0.337
Legume presence x Year	1	39	0.06	0.811
Tall herb presence x Year	1	2636	3.86	0.051
Seed addition x Year	1	778	1.14	0.288
Plot x Subplot Year	*155*	*105942*	*0.31*	*1*
Residual	*160*	*353360*		

Table C5: Analysis of variance (ANOVA) of the total number of species per harvest quadrat and of community biomass (gm^{-2}). Target species were residents in weeded controls (w-), but residents, external and internal invaders in non-weeded subplots (c- and c+). "Species richness" is the sown species richness of the resident community. The weeding and seed addition treatments (w-, c- and c+) were used to form two contrasts. The first of them ("Invasion") represents weeded controls (w-) vs. invasion treatments (c- and c+), the second ("Seed addition") represents non-weeded treatments without seed addition (c-) vs. with seed addition (c+). Error terms are printed in italics.

	Number of species				Biomass			
Source	**df**	**SS**	**F**	**P**	**df**	**SS**	**F**	**P**
Spatial variation	9	1100.7	9.05	<0.001	9	4440201	1.16	0.333
Species richness (log2)	1	3655.3	270.36	<0.001	1	12139477	28.63	<0.001
Species richness (deviation from log-linear)	4	1206.8	22.32	<0.001	4	1651207	0.97	0.428
Plot	*67*	*905.8*	*3.28*	*<0.001*	*67*	*28408418*	*5.88*	*<0.001*
Invasion	1	2915.7	706.83	<0.001	1	5018898	69.59	<0.001
Seed addition	1	203.5	49.34	<0.001	1	251564	3.49	0.064
Species richness (log2) x Invasion	1	289.2	70.10	<0.001	1	1080842	14.99	<0.001
Species richness (deviation from log-linear) x Invasion	4	0.8	0.05	0.995	4	445103	1.54	0.193
Species richness (log2) x Seed addition	1	40.2	9.75	0.002	1	65241	0.90	0.343
Species richness (deviation from log-linear) x Seed addition	4	20.2	1.22	0.303	4	256648	0.89	0.472
Plot x Subplot	*150*	*618.8*	*0.99*	*0.522*	*150*	*10818315*	*0.75*	*0.970*
Year	1	663.5	159.32	<0.001	1	8354184	87.12	<0.001
Species richness (log2) x Year	1	246.6	59.20	<0.001	1	38361	0.40	0.528
Species richness (deviation from log-linear) x Year	4	36.3	2.18	0.072	4	1745162	4.55	0.001
Invasion x Yea	1	357.2	85.75	<0.001	1	1586364	16.54	<0.001
Seed addition x Year	1	114.4	27.46	<0.001	1	61793	0.64	0.423
Species richness (log2) x Invasion x Year	1	87.4	20.98	<0.001	1	59669	0.62	0.431
Species richness (deviation from log-linear) x Invasion x Year	4	7.2	0.43	0.787	4	203245	0.53	0.714
Species richness (log2) x Seed addition x Year	1	12.6	3.02	0.084	1	87566	0.91	0.340
Species richness (deviation from log-linear) x Seed addition x Year	4	5.2	0.31	0.868	4	291002	0.76	0.553
Plot x Subplot x Year	*224*	*932.9*	*2.13*	*<0.001*	*224*	*21480355*	*1.41*	*0.005*
Residual	*242*	*472.5*			*242*	*16501297*		

Table C6: Analysis of variance (ANOVA) of community biomass, including the effect of observed (=realised) species richness. Target species were residents in weeded controls (w-), but residents, external and internal invaders in non-weeded subplots (c- and c+). The influence of "Realised species richness (log_2-transformed)" on community biomass was tested against the interaction "*Plot x Subplot x Year*". The weeding and seed addition treatments (w-, c- and c+) were used to form two contrasts. The first of them ("Invasion") represents weeded controls (w-) vs. non-weeded treatments (c- and c+), the second ("Seed addition") represents non-weeded treatments without seed addition (c-) vs. with seed addition (c+). Error terms are printed in italics.

Source	**df**	**SS**	**F**	**P**
Spatial variation	9	4085251	6.00	0.307
Realised richnes (log2)	1	15619722	160.67	<0.001
Plot	*72*	*36869246*	*6.83*	*<0.001*
Invasion	1	75710	1.01	0.316
Seed addition	1	27015	0.36	0.549
Realised richnes (log2) x Invasion	1	557075	5.73	0.017
Realised richnes (log2) x Seed addition	1	658371	6.77	0.010
Plot x Subplot	*160*	*11987260*	*0.77*	*0.962*
Year	1	3874550	39.85	<0.001
Realised richnes (log2) x Year	1	1850417	19.03	<0.001
Invasion x Year	1	1347	0.01	0.906
Seed addition x Year	1	15993	0.16	0.685
Realised richnes (log2) x Invasion x Year	1	563858	5.80	0.017
Realised richnes (log2) x Seed addition x Year	1	85679	0.88	0.349
Plot x Subplot x Year	*239*	*23234778*	*1.55*	*<0.001*
Residual	*233*	*14571877*		

Table C7: Analysis of variance (ANOVA) of the community biomass, including the effect of observed (=realised) functional group proportions. In this analysis, external invaders were excluded because they could not be grouped into the respective functional groups, so target species in this case were residents in weeded controls (w-), but residents and internal invaders in non-weeded subplots (c- and c+). Three outliers with very high biomass were excluded. The realised functional group proportions were included in the model in the order of their explanatory power and their influence was tested against the "*Residual*". The weeding and seed addition treatments (w-, c- and c+) were used to form two contrasts. The first of them ("Invasion") represents weeded controls (w-) vs. non-weeded treatments (c- and c+), the second ("Seed addition") represents non-weeded treatments without seed addition (c-) vs. with seed addition (c+). Error terms are printed in italics.

Source	**df**	**SS**	**F**	**P**
Spatial variation	9	2609852	2.10	0.041
Proportion of legumes	1	4847743	80.23	*<0.001*
Proportion of small herbs	1	1161391	19.22	*<0.001*
Proportion of grasses	1	1483	0.02	0.876
Plot	*72*	*9961269*	*2.29*	*<0.001*
Invasion	1	3875505	64.14	*<0.001*
Seed addition	1	142731	2.36	0.126
Proportion of legumes x Invasion	1	924491	15.30	*<0.001*
Proportion of small herbs x Invasion	1	41616	0.69	0.408
Proportion of grasses x Invasion	1	256598	4.25	0.041
Proportion of legumes x Seed addition	1	39499	0.65	0.420
Proportion of small herbs x Seed addition	1	9209	0.15	0.697
Proportion of grasses x Seed addition	1	410	0.01	0.934
Residual	*147*	*8882268*		

CHAPTER 4

Effects of plant species loss on aphid–parasitoid food webs

Petermann JS, Müller CB, Weigelt A, Weisser WW, Schmid B, submitted to *Journal of Animal Ecology*

"*Like the insects themselves, we are caught by opposing forces: between the devil of oversimplification on the one hand and a deep blue sea of endless unrelated factors on the other. The important thing is to ensure that neither gets the upper hand.*"
(Lawton and McNeill 1979)

Summary

1. The consequences of species loss on ecosystem functioning within a single trophic level have been extensively studied. However, the loss of basal species is likely to have profound impacts on the abundance, richness and ecosystem functioning of species at higher trophic levels.

2. Here, we used experimentally established plant communities with a species richness gradient to study the effects of plant species loss on a multi-trophic insect food web in the field. We measured densities and species richness of aphids and parasitic wasps (primary, secondary and facultative tertiary parasitoids of aphids) that naturally colonised the grassland plots.

3. Furthermore, we calculated two ecosystem functions: aphid load (the number of aphid individuals per host plant biomass used as a proxy for herbivory) and parasitism rate. We used structural equation models to separate direct from indirect effects of plant species richness on higher trophic levels.

4. We found that the densities and richness of species at all trophic levels were influenced by changes in plant species richness. However, the effects were rarely direct, but instead mediated by the abundance and species richness of aphid host plants and subsequent trophic levels.

5. The herbivore and primary parasitoid levels were most directly affected by changes in plant species richness, with highest insect densities and species richness occurring at intermediate plant species richness. The densities and species richness at the highest trophic levels declined linearly with plant species richness due to a negative response to sparse resources, resulting in reduced trophic structure of food webs in communities with the highest plant species richness.

6. Aphid load was highest at intermediate plant species richness and negatively affected by host plant biomass and host plant species richness. Parasitism rate was mostly affected indirectly via aphid density and overall only weakly negatively affected by plant species richness.

7. We conclude from the observed direct and indirect cascading effects of plant species loss up to at least the fourth food web level that the trophic structure of communities should be taken into consideration when assessing effects of species loss.

Introduction

The consequences of the prevalent loss of species have been thoroughly studied over the past decade. The effect of terrestrial plant species loss on primary productivity has certainly

received most attention, with studies largely in agreement that a decline in plant species negatively affects ecosystem functioning at the plant level (reviewed e.g. by Balvanera *et al.*, 2006; Hooper *et al.*, 2005). However, studies have rarely considered diversity loss in a multi-trophic context (Duffy *et al.*, 2007; Thébault, Huber & Loreau, 2007). For example, the loss of plant species is likely to have profound bottom-up effects via cascading secondary extinctions and subsequent loss of ecosystem function at higher trophic levels (Joshi *et al.*, 2004; Kagata & Ohgushi, 2006; Thébault *et al.*, 2007; Thébault & Loreau, 2006).

In fact, a large number of hypotheses regarding multi-trophic consequences of plant diversity loss exist, but they are often contradictory and rarely reflected in empirical results even for herbivores, the first trophic level above plants. For example, the classical resource concentration hypothesis and the enemies hypothesis (Root, 1973) predict high specialist herbivore loads in low plant diversity due to a concentration of resources and a low efficiency of generalist predators. However, some studies have found exactly the opposite: weaker herbivory in low plant diversity (Prieur-Richard *et al.*, 2002; Scherber *et al.*, 2006), lower herbivore loads with increased host plant abundance (i.e. a resource dilution effect, Koricheva *et al.*, 2000; Otway, Hector & Lawton, 2005) and increased predator efficiency in low plant diversity (Aquilino, Cardinale & Ives, 2005).

The higher the trophic level, the more complex are the predictions for plant diversity effects that have been proposed, especially because effects are often not direct but mediated by other trophic levels (Abrams *et al.*, 1996; Balvanera *et al.*, 2006; Dyer & Letourneau, 2003; Dyer & Stireman, 2003; Siemann *et al.*, 1998; Tscharntke & Hawkins, 2002; Viketoft *et al.*, 2009). For example, direct effects of plant diversity on higher trophic levels could include effects of plant architecture (Brose, 2003; Hochberg & Hawkins, 1992; Langellotto & Denno, 2004; Root, 1973; Vanbergen *et al.*, 2007) or floral resources (e.g. Araj *et al.*, 2008; Langellotto *et al.*, 2004). Indirect effects could be mediated by the density, the species richness or life-history traits (e.g. body size) of species at lower trophic levels (Abrams *et al.*, 1996; Bukovinszky *et al.*, 2008; Knops *et al.*, 1999).

While plant species richness is often assumed to underlie food-web change across habitats (e.g. Albrecht *et al.*, 2007; Macfadyen *et al.*, 2009; Perner *et al.*, 2003; Unsicker *et al.*, 2006) it is rarely explicitly manipulated. However, to disentangle effects of plant species loss and of correlated factors on higher trophic levels, controlled experiments are necessary. Few such experiments have been conducted and the most rigorous ones have been lab experiments (e.g. Aquilino *et al.*, 2005). Field experiments typically only consider one, rarely two, trophic levels above the primary producers (e.g. Haddad *et al.*, 2001; Knops *et al.*, 1999; Koricheva *et*

al., 2000; Mulder *et al.*, 1999; Otway *et al.*, 2005; Prieur-Richard *et al.*, 2002; Scherber *et al.*, 2006; Siemann *et al.*, 1998; Symstad, Siemann & Haarstad, 2000) or focus on single or few plant species out of the entire community (e.g. Prieur-Richard *et al.*, 2002). Furthermore, almost all field studies associate herbivores, predators, parasitoids and plant communities based on co-occurrences (e.g. Haddad *et al.*, 2001; Knops *et al.*, 1999; Koricheva *et al.*, 2000; Siemann *et al.*, 1998), rarely quantifying actual interactions between trophic levels. To address these shortcomings, this study examined quantified aphid–parasitoid food webs comprising three to four trophic levels above plants in a grassland field experiment that directly manipulated plant species richness.

Aphids are attacked by primary parasitoid wasps that lay a single egg into their host's body. The aphids continue to feed for a few days before dying and developing into hard-shelled "mummies" in which the primary parasitoid larva eventually pupates. Two guilds of secondary parasitoid wasps attack primary parasitoids: hyperparasitoids lay their egg into the developing primary parasitoid larva inside the living aphid and delay their development until the primary parasitoid larva has killed the aphid host; they are koinobiont endoparasitoids. Mummy parasitoids, on the other hand, lay their egg onto the primary parasitoid larva inside the dead and mummified aphid; they are idiobiont ectoparasitoids (Godfray, 1994). Because hyperparasitoid larvae have to deal with the primary parasitoid's immune system, they are usually more specialised than mummy parasitoids (Bukovinszky *et al.*, 2008; Müller *et al.*, 1999). Mummy parasitoid larvae can furthermore feed on primary parasitoid larvae and hyperparasitoid larvae (facultative tertiary parasitism, Müller *et al.*, 1999). Thus, mummy parasitoids represent a trophic level slightly above hyperparasitoids, i.e. in our case a facultative fifth level in the food web. With aphids being sedentary herbivores and all parasitoids being solitary (i.e. a single parasitoid developing from a single host), links between food web members can be established and fully quantified.

Aphid–parasitoid food webs are frequently used as ecological model systems for this reason (Müller *et al.*, 1999), but also because they are important in an agricultural context (e.g. Brewer & Elliott, 2004; Schmidt *et al.*, 2003). Herbivory by aphids constitutes a central ecosystem function within the aphid–parasitoid food web, albeit an unpopular one with farmers. The magnitude of herbivory is expected to be highly correlated with herbivore load, i.e. in this case the number of aphids per biomass of the host plant, which we will therefore use as a proxy for herbivory. Parasitism of aphids by parasitic wasps is another ecosystem function in the aphid–parasitoid food web, but one that is promoted by farmers as biocontrol against aphids. These two important ecosystem functions could be affected by changes in

plant diversity, either directly or indirectly via the density or richness of the involved organisms.

Here we report results from 47 quantified aphid–parasitoid food webs associated with experimental plant communities of varying plant species richness and test the following hypotheses: (1) the loss of plant species affects densities and species richness of all trophic levels; (2) the loss of plant species has strong direct effects on lower trophic levels with indirect effects cascading up the food web; (3) ecosystem functions at higher trophic levels, such as herbivory (herbivore load) and parasitism are affected by a loss of plant species.

Material and Methods

The present study was conducted at the site of the Jena Experiment, a large grassland biodiversity–ecosystem functioning experiment in Jena, Germany (Roscher *et al.*, 2004). This experiment was established in 2002 on a former agricultural field in the floodplain of the Saale river. The plant species pool of the experiment used for this study contained nine dominant species from semi-natural, species-rich, mesophilic grassland typical of the area (Roscher *et al.*, 2004; Roscher *et al.*, 2005). The 3.5 x 3.5 m plots did not receive fertiliser but were mown twice a year in June and September, a typical management regime for these grasslands. Among the nine species were five grasses (*Alopecurus pratensis, Arrhenatherum elatius, Dactylis glomerata*, *Phleum pratense*, *Poa trivialis*, all plant nomenclature follows Rothmaler (2002)), two forbs (*Anthriscus sylvestris, Geranium pratense*) and two legumes (*Trifolium pratense, Trifolium repens*). Species richness levels were 1, 2, 3, 4, 6, and 9 plant species. Spontaneously colonising plant species were removed by weeding to maintain the original species compositions. The plots were arranged into four blocks (for details regarding the design see Roscher *et al.*, 2004; Roscher *et al.*, 2005). Aphids naturally colonised four of the nine plant species in the experiment (*A. elatius, P. pratense, A. sylvestris, T. pratense*), so we randomly selected 47 plots containing at least one of these plant species at an abundance of >5% (based on cover estimates in May 2006). These were seven monocultures, 19 two-species mixtures, seven three-species mixtures, seven four-species mixtures, four six-species mixtures and three nine-species mixtures (Table S1).

Data collection

We counted naturally occurring aphids and collected parasitized aphids (mummies) four times from May (first appearance of aphids at the field site) to August 2006 (almost no aphids found after the fourth sampling period). Sampling was usually completed within one week and was

carried out twice before the first mowing of the field site (around 2 June and 17 June) and twice between the first and the second mowing (20 July and 2 August). After the initial identification of all aphid species in the lab, aphids were identified in situ and counted on all plants along a transect of 3 x 0.2 m across the middle of the plot. Mummies were collected in the same transects at the same time and, additionally, in a larger area (usually 1.1 x 3.5 m) to be able to detect the entire parasitoid community of a plot. Mummies were placed individually in gelatine capsules and kept in the lab until the emergence of the parasitoid. After three months at room temperature, non-emerged mummies were subjected to two cold (4°C) periods of one month with a warm period of one month in-between to induce emergence. All emerged parasitoids were identified to species level under a binocular microscope using specialist keys (e.g. Fergusson, 1980; Japoshvili & Abrantes, 2006; Kavallieratos *et al.*, 2005; Starý, 1966, 1976). Plant biomass was harvested in two randomly selected areas of 20 x 50 cm in the plots in May and August, just before mowing. The biomass was sorted to species level, dried and weighed (for a detailed description of the harvest methods see Marquard *et al.*, in press; Roscher *et al.*, 2005).

Data analysis

Plant biomass, separated into the different host and non-host plant species, was summed over the whole season. Densities of aphids, primary parasitoids, hyperparasitoids and mummy parasitoids were used as sums over all sampling dates in the analyses but are shown separately for the sampling dates in Fig. 1. "Species richness" is the total number of species in each group in the sampled area over all sampling dates. Two ecosystem functions of the aphid–parasitoid food web were considered in this study: aphid herbivory and parasitism. Because the effect of sucking insects on plants cannot be measured directly, aphid load (the number of aphid individuals per host plant biomass) was used as a proxy for herbivory. Parasitism rate (the proportion of parasitized aphids) was calculated as number of all parasitoids divided by the sum of the number of aphids and parasitoids. Secondary parasitoids were included in this rate because mummies from which secondary parasitoids emerged had originally been parasitized by primary parasitoids. Insect densities and richness were square-root transformed, aphid load and parasitism rate were arcsine-square-root transformed prior to statistical analyses. Plot means of host plant biomass, insect densities and host plant and insect richness were analysed using multiple regression and analysis of variance (ANOVA, for more details on statistical analyses in biodiversity experiments, see Schmid *et al.*, 2002).

The following model was used for all response variables: "response variable" ~ "block" + "plant species richness" + "(plant species richness)^2".

Structural equation models (Hair *et al.*, 1995) were used to separate direct and indirect effects of plant species richness on organisms and ecosystem functions at higher trophic levels. For these analyses, four *a priori* models were constructed: one for the effect of plant species richness on insect densities (Fig. S1), one for the effect of plant species richness on insect species richness (Fig. S1), one for the effect of plant species richness on aphid load (Fig. S2a) and one for the effect of plant species richness on parasitism rate (Fig. S2b). The first two models included all possible direct and indirect bottom-up paths to higher trophic levels. The only exception was the variable "(plant species richness)^2" which we only expected (after the first analyses) to have an influence on aphids and primary parasitoids. Furthermore, we included covariances between mummy parasitoids and hyperparasitoids and between plant species richness and "(plant species richness)^2". The initial models for aphid load and parasitism rate were based on the results from the models for densities and species richness and only the initial model for aphid load contained a path from "(plant species richness)^2" to aphid load. All initial models were based on correlation matrices and then simplified by deleting the least significant paths and comparing resulting nested models with the previous model (Anderson & Gerbing, 1988). Model simplification was continued until BIC (Bayesian Information Criterion, Johnson & Omland, 2004) scores increased compared with the previous model. Final models were evaluated by several goodness-of-fit statistics, such as the Tucker-Lewis Non-Normed Fit Index and the Comparative Fit Index (Hair *et al.*, 1995).

Data were analysed with the free software R, version 2.7.2 (R Development Core Team, http://www.r-project.org), including the sem package version 0.9-12 for structural equation modelling (Fox, 2006).

Results

Aphids were parasitized by chalcidoid and ichneumonoid wasps, secondary parasitoids included cynipoid, chalcidoid and ceraphronoid wasps (complete species list in Table S2). In the study year, aphids appeared at the end of May after a cold spring (Fig. 1). Aphid densities peaked shortly before the first mowing in June and increased again after plants had re-grown. The last aphids were observed on the plots shortly after the end of the fourth sampling period at the beginning of August. Primary parasitoid densities remained relatively constant throughout the year while secondary parasitoid densities showed a peak in June. Aphids and associated parasitoids were found on four host plant species in differing densities (Table 1),

with highest aphid densities (individuals/m^2) on *Phleum pratense* and highest parasitoid densities on *Anthriscus sylvestris*. Only aphids on *P. pratense* were found throughout the season, all other aphids were restricted to one or two sampling dates. Almost all insect species in the food webs proved to be monophagous; very few species were oligophagous during our study. In total, ten aphid species, eight primary parasitoid species, seven hyperparasitoid species and seven mummy parasitoid species were found, with the highest aphid and parasitoid richness and the highest parasitism rate on *A. sylvestris.*

Overall effects of plant diversity

Host plant species richness (hereafter "host plant richness") increased with increasing overall plant species richness (hereafter "plant richness") as a feature of the experimental design. In contrast, total host plant biomass in the plots decreased linearly with increasing plant richness (Fig. 2, Table 2). Aphid and primary parasitoid densities tended to show a unimodal relationship with plant richness, with maximum densities at intermediate plant richness levels (Fig. 3, Table 2). Hyperparasitoid density was negatively affected by plant richness while mummy parasitoid density showed no relationship with plant richness. Aphid and primary parasitoid richness were again a unimodal function of plant richness, hyperparasitoid richness decreased linearly and mummy parasitoid richness did not change with changing plant richness. Ecosystem functioning in terms of aphid load and parasitism rate showed unimodal (aphid load) or weakly negative (parasitism rate) relationships with plant richness (Fig. 4). The effect of the presence of legumes in plant communities was tested as a separate contrast in initial analyses because this particular plant functional group has been shown to influence ecosystem functioning in terms of biomass production (e.g. Spehn *et al.*, 2002) and life-history characteristics of aphids and parasitoids (Chapter 5). However, legumes did not have important effects in any of the present analyses, and thus the term was removed from the models.

Direct and indirect effects of plant diversity

Using structural equation modelling, we separated effects of plant richness on higher trophic levels into direct and indirect effects. After sequential deletion of non-significant terms from the initial *a priori* models (Figs S1 and S2), we arrived at models with minimal BIC scores and adequate fit (Hair *et al.*, 1995). According to the most parsimonious model for the effects of plant richness on insect densities (Fig. 5a) all significant effects on higher trophic levels were indirect. Plant richness had an indirect positive effect on host plant biomass via

increased host plant richness but a strong direct negative effect, resulting in the weak negative overall effect of plant richness on host plant biomass (Fig. 2b). Aphid density was positively influenced by primary parasitoid density which in turn was positively influenced by densities of both groups of secondary parasitoids. There was no significant quadratic effect of plant richness.

In contrast, insect species richness was not affected by changes in host plant biomass (Fig. 5b). Here, plant richness and host plant richness directly and indirectly influenced higher trophic levels. The effects were strongest at the herbivore level. Plant richness had a direct quadratic effect on aphid richness that resulted in the unimodal relationship (Fig. 2e). At the same time, host plant richness had a strong positive linear effect on aphid richness. In general, species richness at trophic levels directly below the respective insect group showed strong positive influences, whereas direct effects from lower levels were either weakly positive or negative. The signs for direct and indirect effects were often opposing, leading to weak overall effects.

Aphid load was influenced by a number of variables in the food web and also showed a direct linear and quadratic effect of plant richness, a negative effect of host plant richness and host plant biomass and a positive effect of aphid density (Fig. 6a). Aphid richness did not influence aphid load. Parasitism rate was expectedly strongly affected by primary parasitoid density and aphid density (Fig. 6b). However, there was an additional negative effect of host plant richness and a positive effect of primary parasitoid richness on parasitism rate. Plant richness had no direct effect on parasitism rate; instead indirect positive and negative effects nearly cancelled each other out, resulting in a weak negative overall effect of plant richness on parasitism rate (Fig. 4b).

Food webs

Above, we presented separate structural equation models for the effects of plant richness on insect densities and on insect species richness. However, insect density and species richness were correlated at each trophic level (Fig. 7).The higher the trophic level, the steeper the slope of the density–richness relationship on the log–log scale, i.e. the more species were lost with a similar decline in density. Food-web graphs that were drawn separately for each plant richness level (Fig. 8) illustrate the consequences of these density–richness relationships for the entire webs. With increasing plant richness and associated declines in host plant biomass, the densities of insects at higher trophic levels also declined (see also Fig. 3). The higher the trophic level, the earlier this decline in abundance set in and the faster the species were lost.

The most dramatic change could be seen in the six- and nine-species mixtures, where first the facultative tertiary parasitoids (mummy parasitoids) and then the secondary parasitoid level disappeared completely. Food web properties such as link density (number of links per species) and connectance (number of links per possible links) were calculated (Bersier, Banasek-Richter & Cattin, 2002). However, because all insect species proved to be highly host-specific at the field site during the study year, most food web properties were strongly correlated with the number of species in the food web and are not presented.

Discussion

Aphid density and species richness

Confirming our first hypothesis, plant richness in artificially established communities affected higher trophic levels of plant–aphid–parasitoid food webs in the field. Furthermore, plant richness had more direct and stronger effects on lower levels of the food web, confirming our second hypothesis. Previous studies have found both positive and negative effects of plant richness on herbivore density, richness and on herbivory (e.g. Jactel & Brockerhoff, 2007; Knops *et al.*, 1999; Siemann *et al.*, 1998; Unsicker *et al.*, 2006). Nevertheless, most studies agree that specialist herbivores are predominantly controlled by the presence, density and richness of their host plants (Jactel *et al.*, 2007; Joshi *et al.*, 2004; Koricheva *et al.*, 2000; Otway *et al.*, 2005). Indeed, we found that the density of aphids, a relatively specialised group of herbivores, was mainly driven by the biomass of their host plants. Overall, the opposing direct and indirect effects at the plant level resulted in hump-backed relationships of aphid density and aphid richness with plant richness; i.e. intermediate plant richness was most favourable for aphids. At the lower end of the plant richness gradient, they seemed to benefit from an increase in host plant richness. Towards the higher end, they were increasingly limited by low host plant biomass and potentially by the additional structure of non-host plants affecting the searching efficiency of winged aphid colonisers (e.g. Joshi *et al.*, 2004). This conclusion is supported by the fact that aphids are generally inefficient at locating host plants (Dixon *et al.*, 1987). However, we interpret the data with caution because we sampled few species-rich plant communities and therefore, our data set is unbalanced with respect to the plant richness gradient.

Whilst this study focussed on bottom-up effects of plant richness on higher trophic levels, herbivores are not only controlled by their food plants but also by their predators and parasitoids (Hairston, Smith & Slobodkin, 1960; Lawton & McNeill, 1979). To assess the strength of these top-down effects and interactions between bottom-up and top-down forces,

experiments that simultaneously manipulate species richness at lower and higher trophic levels are necessary. So far such experiments have been scarce (but see Aquilino *et al.*, 2005) and they are especially challenging to carry out in a field setting.

Parasitoid density and species richness

We found that all higher trophic levels were influenced by changes in plant richness in our study, but rarely in a direct way. Densities of primary and secondary parasitoids were strongly dependent on the densities of their food sources. Likewise, primary and secondary parasitoid richness were driven by the species richness of their prey. Hence, their relationship with plant richness largely followed the relationship of aphid density and richness with plant richness. Richness-mediated indirect effects were typically stronger than density-mediated indirect effects, which is in accordance with findings of previous studies (Knops *et al.*, 1999; Siemann *et al.*, 1998).

Plant richness had a negative overall effect on the highest trophic levels in our food webs, which was partly obscured by the indirect interactions. While density and richness within a trophic level were strongly correlated for all trophic levels, the higher the trophic level, the more species were lost with a similar decline in density (steeper slopes of the density–richness correlations for primary and secondary parasitoids). Parasitoid densities in our plots were generally low: with a plot size of about 12 m^2, the resulting parasitoid populations in each plot were usually supported by less than 100 newly emerging primary parasitoid individuals and even less secondary parasitoids over all sampling dates. When plant richness increased beyond a certain threshold, parasitoid densities dropped to very low levels and parasitoid species richness declined rapidly. The highest trophic level, secondary parasitoids, disappeared altogether in the communities with the highest plant richness, indicating a disassembly of food webs from the top as a result of low population sizes (Srivastava & Lawton, 1998).

While bearing the low sample size for communities with a high plant richness in mind, it still seems reasonable to believe that aphid population sizes in the 3.5 x 3.5 m patches of plant communities in our experiment were too low to sustain stable populations of specialist parasitoids. Furthermore, inter-patch connectance that could have stabilised parasitoid populations was probably hampered by the low detectability of small host populations in high surrounding plant richness, creating refuges for aphids (Hochberg *et al.*, 1992). In a parallel study, we found that parasitoid emergence success and proportions of females decreased with

increasing plant richness (Chapter 5). This could have contributed to the observed decline in parasitoid population sizes.

All insect species in our food webs behaved as specialists. Aphids are a relatively specialised group of herbivores in general, and parasitoids typically show narrower host ranges than predators (Memmott, Martinez & Cohen, 2000). However, the species we found may prove to be more generalised than in our study if communities are followed across several years (Petanidou *et al.*, 2008). The results we obtained, especially the strong dependency of food webs on specific aphid host plants and the associated extinctions at higher trophic levels in high plant richness, obviously only apply to the specialised aphid–parasitoid sub-web within the total arthropod community.

Ecosystem functioning

In addition to the effects of plant richness on insect density and richness we measured the effects of plant richness on two ecosystem functions of the aphid–parasitoid system: aphid load and parasitism rate. Confirming our third hypothesis, these functions were influenced by plant species richness. Similar to density and species richness of aphids, aphid load showed a unimodal relationship with plant richness. Furthermore, aphid load was negatively affected by host plant biomass and host plant richness but positively by plant richness, at least at lower plant richness levels. Previous studies have suggested that herbivore load or herbivory increase with host plant abundance due to the improved detectability of abundant hosts (the resource concentration hypothesis, Root, 1973) and consequently decrease with plant richness (Knops *et al.*, 1999). This hypothesis was sometimes used to explain devastating insect infestations in agricultural monocultures (e.g. reviewed by Andow, 1991). However, the opposite, a decrease in herbivore loads with increasing host plant abundance, has recently been found in a biodiversity experiment (a resource dilution effect, Otway *et al.*, 2005). In our study, aphid densities were positively influenced by host plant biomass but densities did not increase proportionally with host plant biomass, thus aphid load declined with increasing host plant biomass, consistent with a resource dilution effect (Joshi *et al.*, 2004; Otway *et al.*, 2005). Population growth effects could be responsible for this result (Otway *et al.*, 2005). Species-specific searching efficiency and arrival events could also explain the decreased herbivore load but these effects would have been masked in our community-level study.

Parasitism rate tended to decline with increasing plant richness and was negatively affected by host plant richness in our study, potentially as a result of decreased parasitoid searching efficiency or aphid quality (Chapter 5). Furthermore, parasitism rate was negatively

influenced by the density of hosts, indicative of a resource dilution effect at a higher trophic level. Aphid species richness did not have a clear effect on parasitism rates, even though resource diversity could be expected to influence ecosystem functioning at the next trophic level. However, this influence could either be positive due to an increased resource partitioning potential (Tylianakis *et al.*, 2008) or negative due to a stronger resistance or decreased parasitoid efficiency (Montoya, Rodriguez & Hawkins, 2003; Schmid *et al.*, 2009; Vos *et al.*, 2001). Possibly, opposing mechanisms were operating simultaneously in our study. Indeed, primary parasitoids appeared to exhibit niche complementarity or facilitation because higher primary parasitoid species richness increased parasitism rates (Aquilino *et al.*, 2005; Cardinale *et al.*, 2003).

In summary, we have shown that plant richness can influence all trophic levels of an aphid–parasitoid food web. Whereas effects of plant richness on herbivore density and richness were direct and easily detectable, effects at higher trophic levels were generally mediated by lower trophic levels and obscured by positive and negative interactions between the respective organisms. Interestingly, food webs started to disassemble from the top in communities of high plant richness, due to the resource limitation and subsequently low population sizes of species at high trophic levels. As a result of changes in aphid and parasitoid density and richness, ecosystem functions performed by these insects were affected by plant species loss.

The results we obtained from experimental grasslands could be applied to agricultural settings, where, for example, promoting the species richness of the parasitoid community could provide benefits in terms of aphid biocontrol. One of our main findings is that bottom-up effects of plant species loss may cascade up to at least the fourth trophic level of associated food webs. Thus, the assessment of effects of species loss on ecosystems should take multi-trophic interactions into account. In conclusion, very low plant richness is not only detrimental to ecosystem functioning at the plant level (Hooper *et al.*, 2005) but also involves smaller and poorer aphid–parasitoid food webs. However, in patchy grassland communities of high plant richness, specialist insect populations experience a higher risk of extinction due to low host abundance. Increasing habitat area and avoiding fragmentation is therefore essential to maintain stable insect populations and species-rich aphid–parasitoid food webs.

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Figures

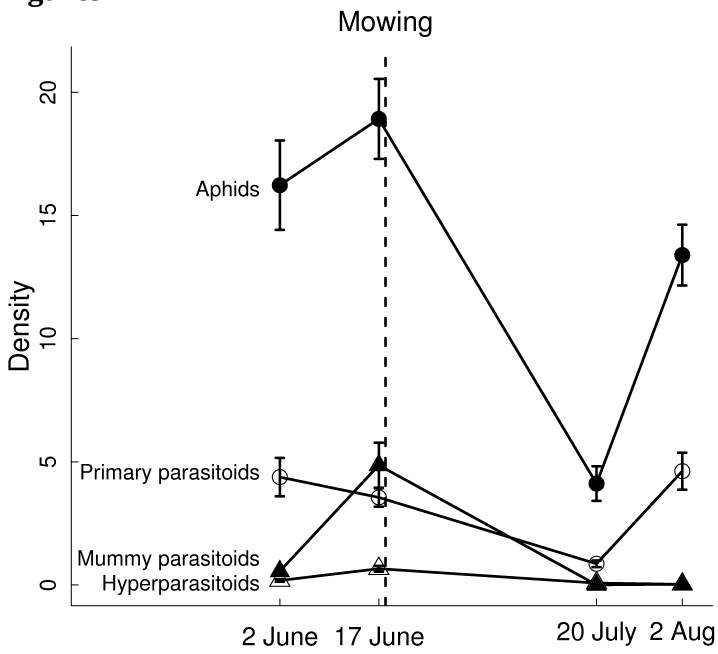


Fig.1: Mean insect density (individuals per m^2) ± SE for the four sampling periods in 2006 in all sampled plots. Aphids: filled circles (actual density scaled down by one order of magnitude), primary parasitoids: open circles, mummy parasitoids: filled triangles, hyperparasitoids: open triangles. The date of the mowing is indicated by a dashed line.

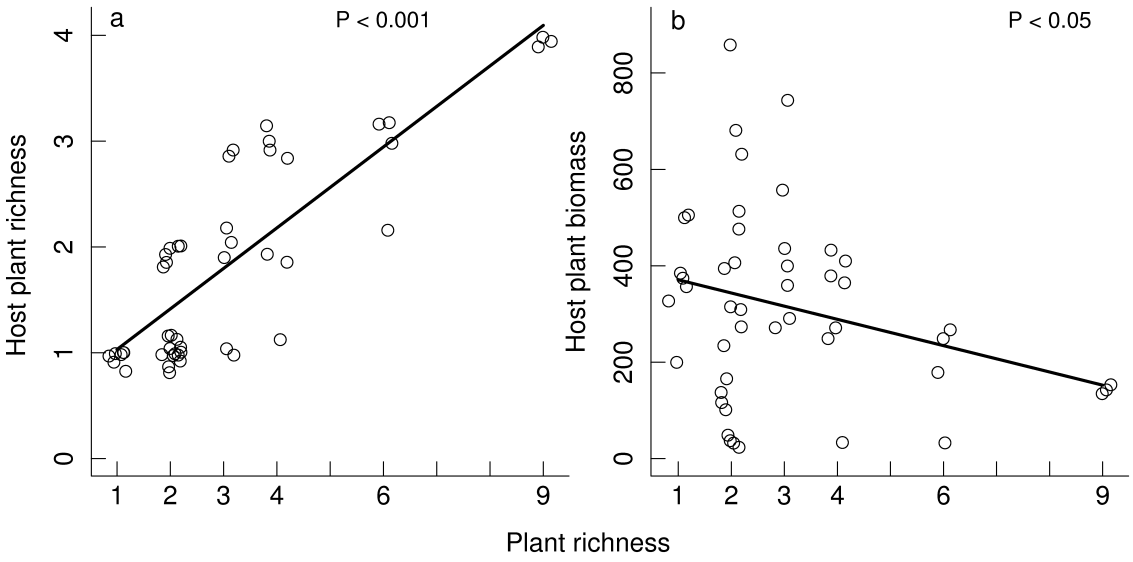


Fig. 2: a) Host plant richness and b) host plant biomass as a function of overall plant richness in the plots. For statistical analyses see Table 2.

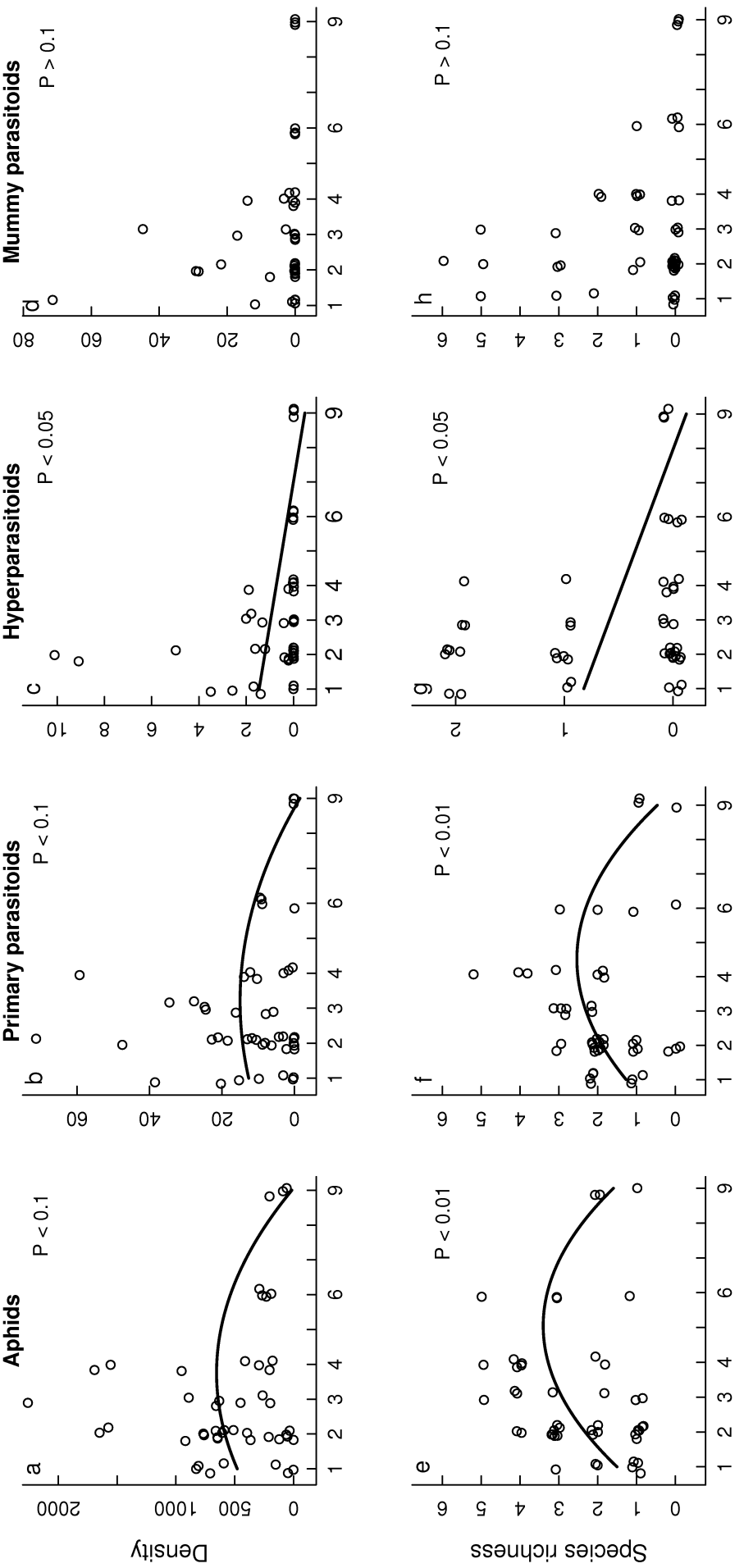


Fig. 3: Density (individuals per m^2) and species richness of aphids, primary parasitoids and secondary parasitoids (hyperparasitoids and mummy parasitoids) as a function of plant richness in the plots. Note the different scale of axes for the different trophic levels. Fitted lines are drawn for relationships significant at P<0.1. Untransformed data are shown but P-values refer to transformed data. For statistical analyses see Table 2.

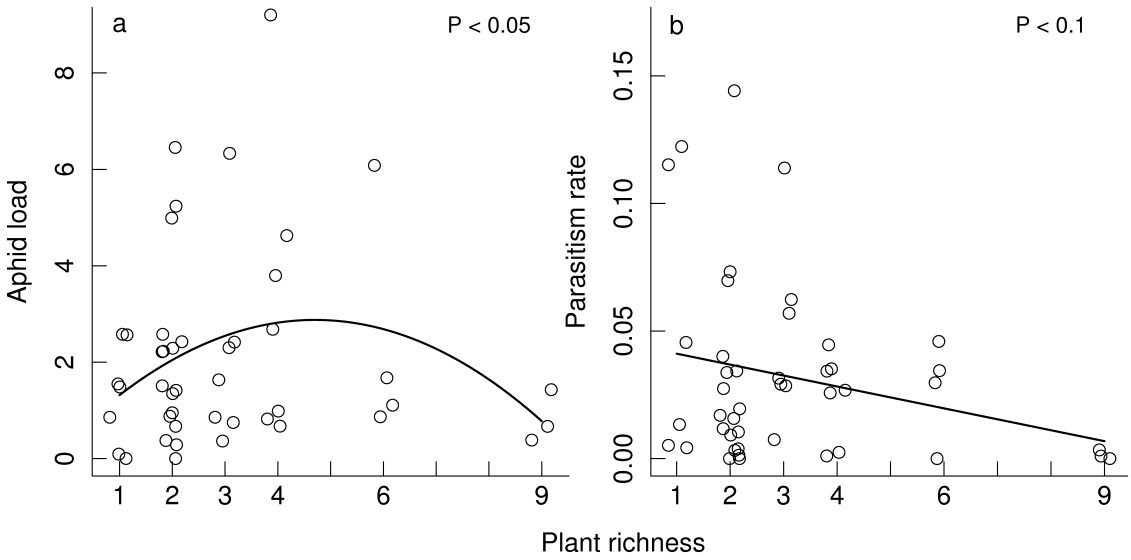
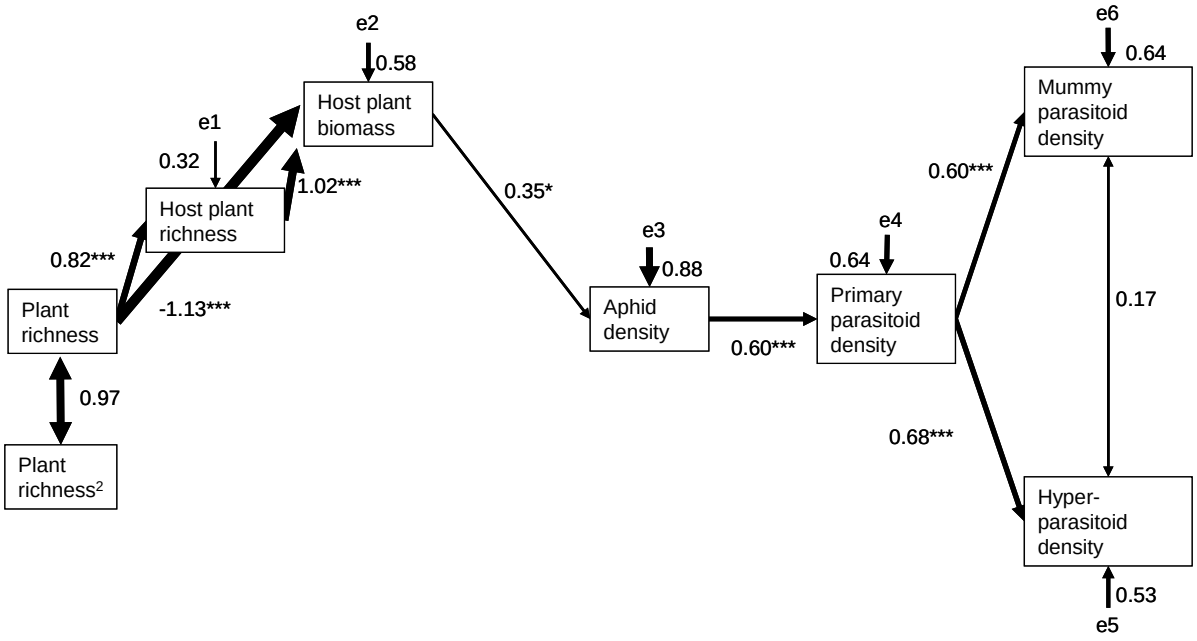


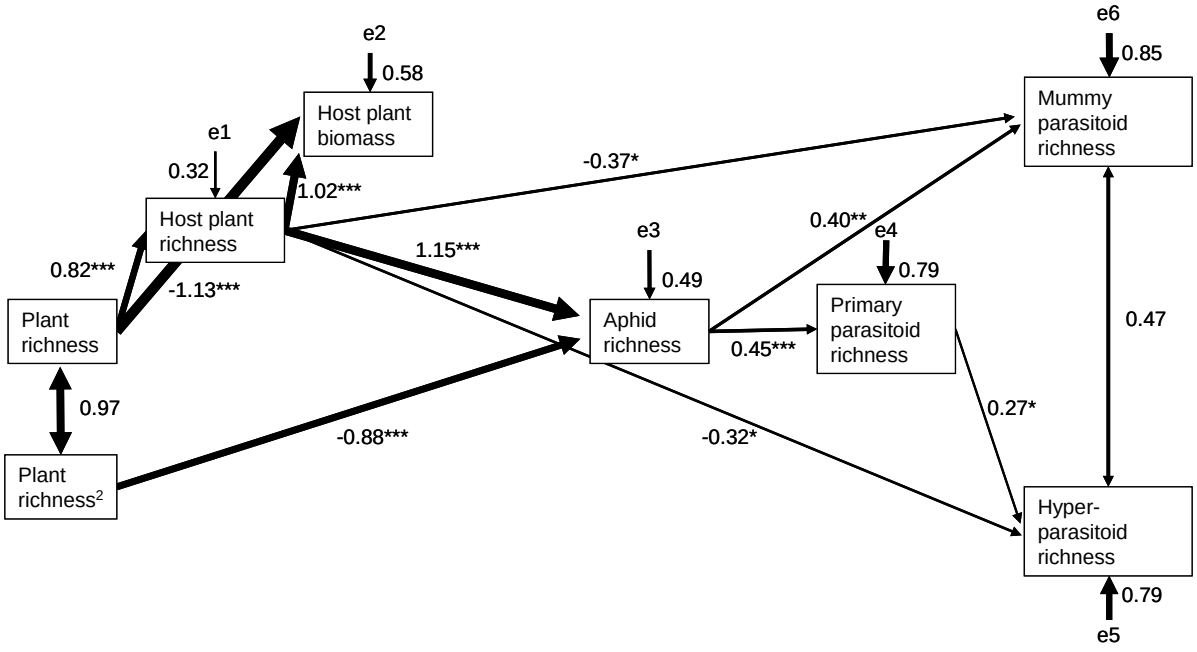
Fig. 4: a) Aphid load (aphid individuals per host plant biomass) and b) parasitism rate (proportion of parasitized aphids) as a function of plant richness in the plots. Fitted lines are drawn for relationships significant at P<0.1. Untransformed data are shown but P-values refer to transformed data. For statistical analyses see Table 2.

a



Chi^2 = 19.4, df = 19, P = 0.43, GFI = 0.91, NNFI = 0.98, CFI = 0.998

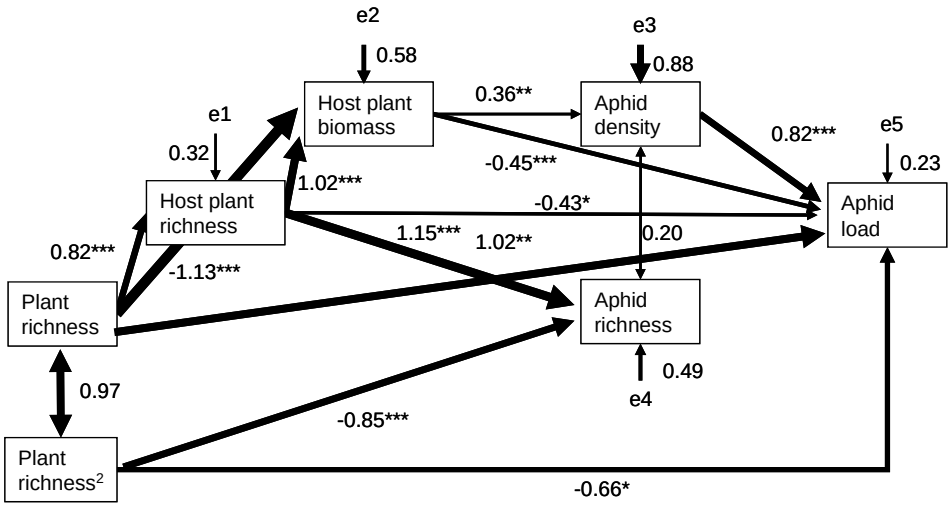
b



Chi^2 = 19.7, df = 16, P = 0.23, GFI = 0.91, NNFI = 0.98, CFI = 0.987

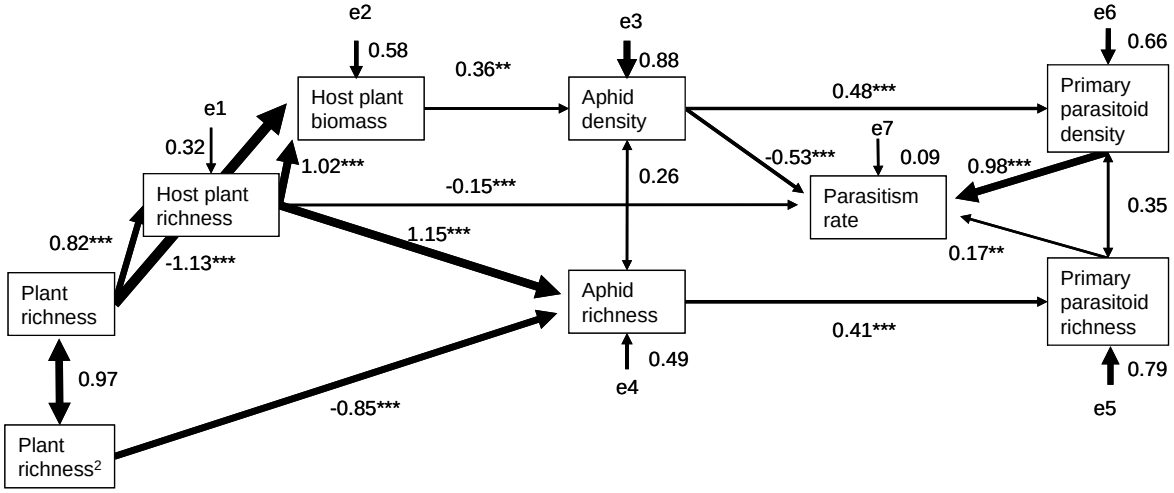
Fig. 5: Final, most parsimonious structural equation models for plant richness effects on a) insect density and b) insect species richness. Insect density and species richness were square-root transformed. Standardized path coefficients are given next to path arrows with significance depicted by * P<0.05, ** P<0.01, *** P<0.001. Unexplained variance is denoted by "e", double-headed arrows indicate covariance. All arrow widths are proportional to path coefficients. For initial *a priori* models see Fig. S1. GFI: Goodness-of-Fit Index, NNFI: Tucker-Lewis Non-Normed Fit Index, CFI: Comparative Fit Index.

a



Chi^2 = 7.4, df = 6, P = 0.49, GFI = 0.96, NNFI = 1.0, CFI = 1.000

b



Chi^2 = 23.0, df = 21, P = 0.35, GFI = 0.90, NNFI = 0.99, CFI = 0.995

Fig. 6: Final, most parsimonious structural equation models for plant richness effects on a) aphid load (aphid individuals per host plant biomass) and b) parasitism rate (proportion of parasitized aphids). Insect density and species richness are square-root transformed, aphid load and parasitism rate are arcsine-square-root transformed. Standardized path coefficients are given next to path arrows with significance depicted by * P<0.05, ** P<0.01, *** P<0.001. Unexplained variance is denoted by "e", double-headed arrows indicate covariance. All arrow widths are proportional to path coefficients. For initial *a priori* models see Fig. S2. GFI: Goodness-of-Fit Index, NNFI: Tucker-Lewis Non-Normed Fit Index, CFI: Comparative Fit Index.

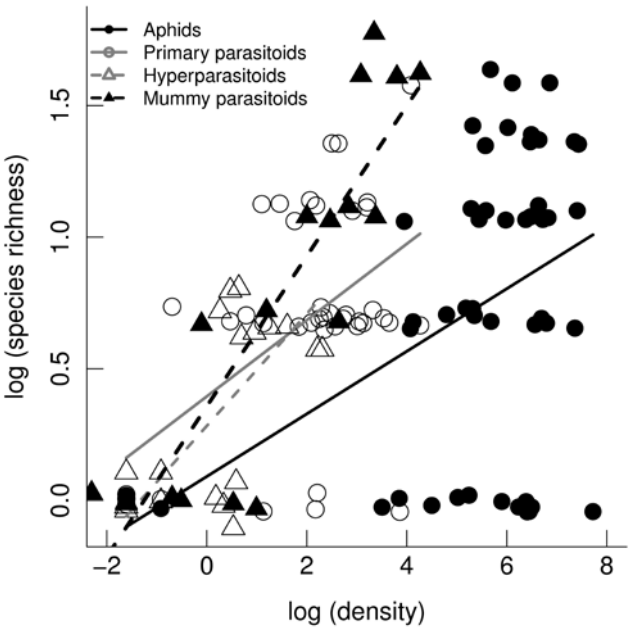


Fig. 7: Density–species richness relationships for the four insect groups on a log–log scale. Aphids: filled circles and black line, primary parasitoids: open circles and grey line, hyperparasitoids: open triangles and dashed grey line, mummy parasitoids: filled triangles and dashed black line. Fitted lines are drawn over the observed ranges of density.

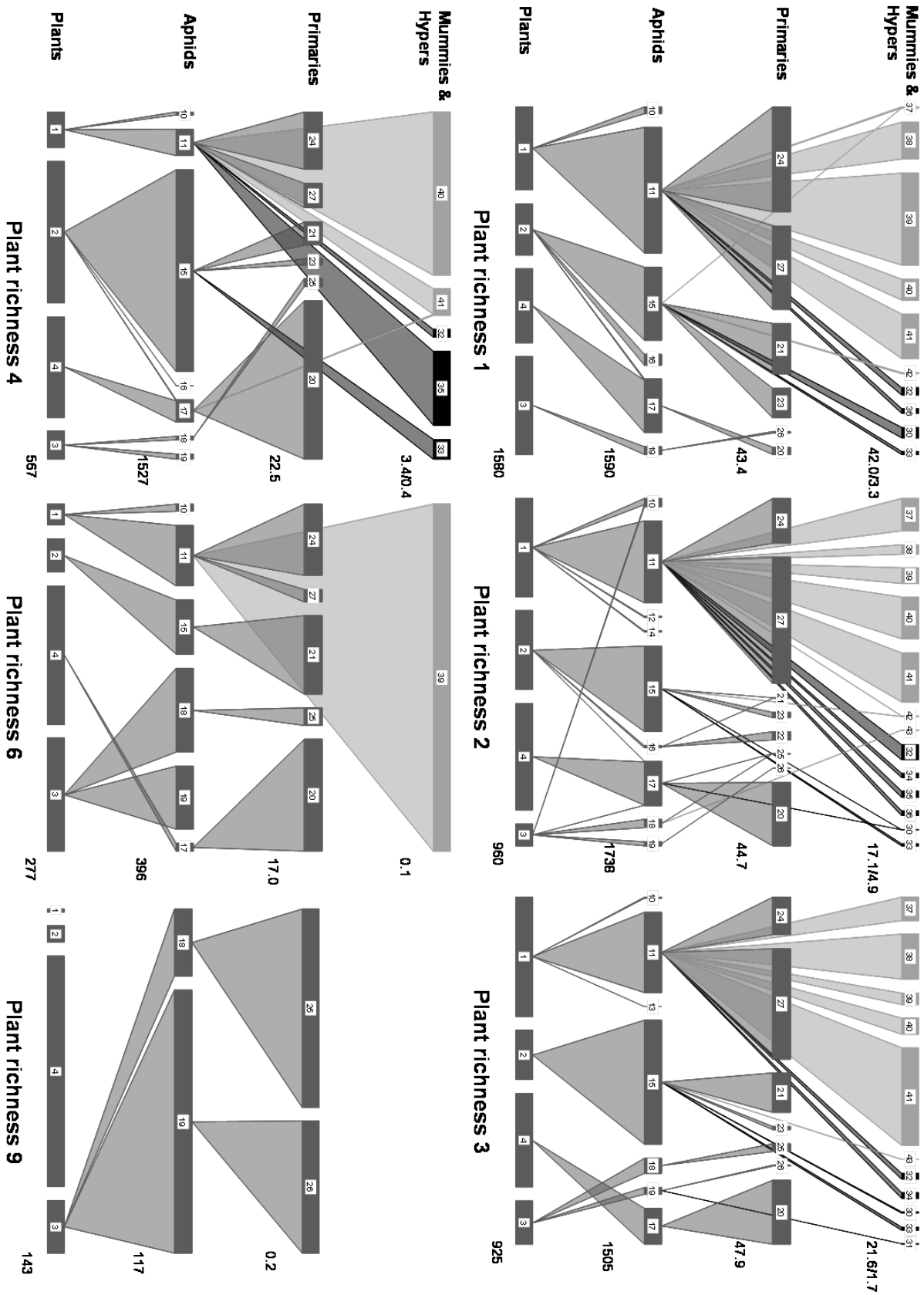

Mummies & Hypers
Primaries
Aphids
Plants
Plant richness 1
1580
1590
43.4
42.0/3.3
Plant richness 2
960
1738
44.7
17.1/4.9
Plant richness 3
925
1505
47.9
21.6/1.7
Plant richness 4
567
1527
22.5
3.4/0.4
Plant richness 6
277
396
17.0
0.1
Plant richness 9
143
117
0.2

Fig. 8: Aphid–parasitoid food webs for the different plant richness levels. The lowest level depicts plants, the second level aphids, the third level primary parasitoids ("Primaries"), the fourth level secondary parasitoids (mummy parasitoids in light grey ("Mummies"), hyperparasitoids in black ("Hypers")). Bar widths represent relative abundances at the respective level. Numbers within bars stand for species names (see Supplementary Table S2). The width of the wedges illustrates link strength. Secondary parasitoid species are linked directly to aphid species because it was not possible to relate secondary parasitoids to the respective primary parasitoid species they had consumed. The data are averaged over all plots at the respective plant richness level. Sample sizes are given in Table S1. Absolute densities (host plant biomass per m^2 or insect individuals per m^2) of all species at the respective level are shown to the right of each web (for secondary parasitoids separately: mummy parasitoid density / hyperparasitoid density).

Tables

Table 1: Mean densities ± standard errors (individuals per m^2) of insects on the four host plants; sums over all sampling dates.

Plant species	Aphids	Primary parasitoids	Hyper-parasitoids	Mummy parasitoids
Anthriscus sylvestris	317 ± 77	14.6 ± 3.7	1.19 ± 0.46	11.56 ± 3.89
Arrhenaterum elatius	168 ± 49	8.3 ± 3.1	0.02 ± 0.02	0.02 ± 0.02
Phleum pratense	545 ± 132	4.9 ± 1.2	0.78 ± 0.48	0.06 ± 0.04
Trifolium pratense	109 ± 20	1.3 ± 0.5	0.01 ± 0.01	0.01 ± 0.01

Table 2: Summary of regression models (with normal errors and identity link) testing the linear and quadratic effects of plant richness on the density and species richness of the organisms in the food web and on ecosystem functions (aphid load and parasitism rate). The model formula was in all cases: "response variable" ~ "block" + "plant species richness" + "(plant species richness)^2". Regression models with other errors and link functions (poisson models with log link for insect density and insect species richness, binomial models with logit link for aphid load and parasitism rate) produced similar results. P values < 0.1 are printed in bold. "Res. df": residual degrees of freedom, "%SS": percent sum of squares explained.

		plant richness			(plant richness)2		
response	**res. df**	**% SS**	**F**	**P**	**% SS**	**F**	**P**
Density							
Total host plant biomass	43	9.0	4.57	**0.038**	0.2	0.09	0.768
Aphids	43	3.4	1.66	0.204	6.9	3.37	**0.073**
Primary parasitoids	43	6.5	3.20	**0.081**	6.3	3.12	**0.084**
Hyperparasitoids	43	9.6	4.63	**0.037**	0.8	0.40	0.530
Mummy parasitoids	43	4.0	1.82	0.185	0.1	0.03	0.871
Species richness							
Host plants	43	67.2	96.57	**0.000**	0.4	0.61	0.439
Aphids	43	1.6	0.90	0.348	19.5	10.97	**0.002**
Primary parasitoids	43	2.1	1.10	0.300	15.3	7.94	**0.007**
Hyperparasitoids	43	10.5	5.06	**0.030**	0.1	0.04	0.852
Mummy parasitoids	43	3.4	1.57	0.217	1.9	0.86	0.360
Function							
Aphid load	41	0.0	0.01	0.919	10.8	5.05	**0.030**
Parasitism rate	41	8.3	3.89	**0.055**	2.4	1.12	0.297

Supporting Information

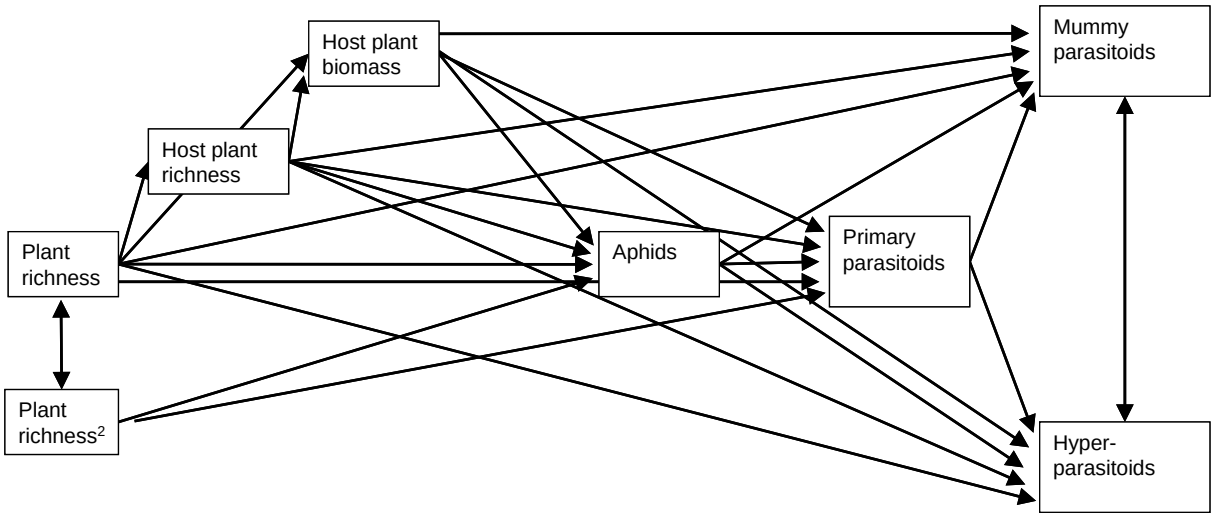
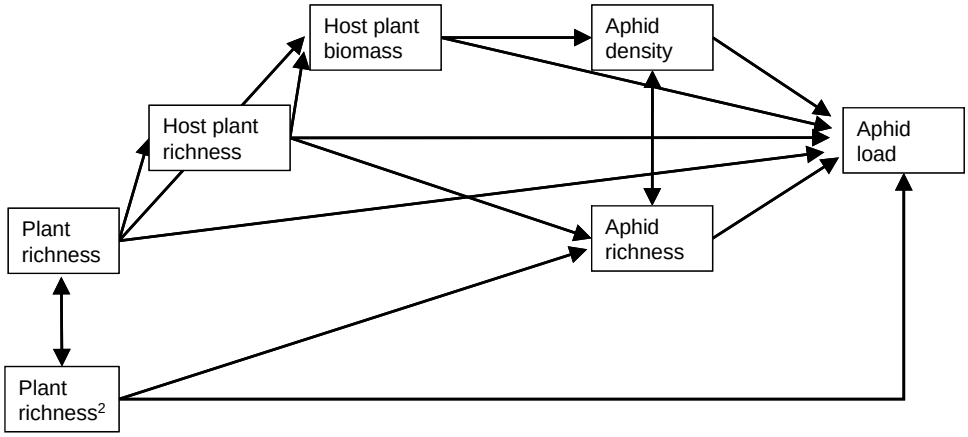


Fig. S1: Initial *a priori* model for effects of plant richness on insect densities or insect species richness. Insect densities and richness were square-root transformed. Double-headed arrows indicate covariance. The final most parsimonious model for species densities is presented in Fig. 5a, the final most parsimonious model for species richness in Fig. 5b.

a



b

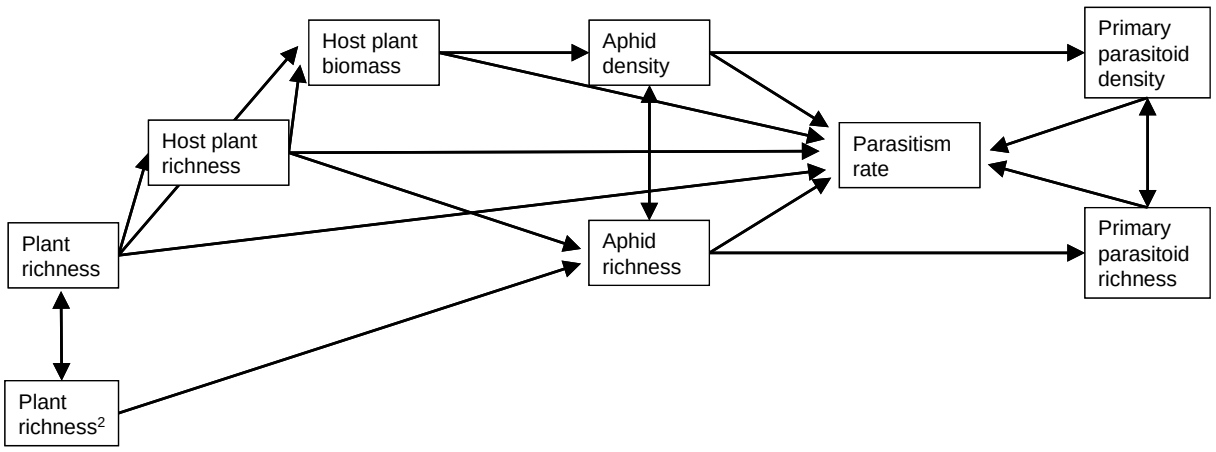


Fig. S2: Initial *a priori* model for effects of plant richness on a) aphid load (aphid individuals per host plant biomass) and b) parasitism rate (proportion of parasitized aphids). Insect densities and species richness were square-root transformed, aphid load and parasitism rate were arcsine-square-root transformed. Double-headed arrows indicate covariance. The final most parsimonious models are presented in Fig. 6.

Table S1: List of all 47 sampled plots with their block number, plot number, composition code, plant species richness, the presence of legumes, the presence of the nine plant species in the plant assemblage and the total host plant biomass (sum across all host plant species and both harvests in 2006). In some cases, replicate plots with the same plant composition were used (same composition codes). The presence of a plant species refers to its presence in the seed mixture at plot establishment in 2002, independent of its actual abundance through 2006. Only the first four plant species hosted aphids in our study. *Ant*: *Anthriscus sylvestris*, *Arr*: *Arrhenatherum elatius*, *Phl*: *Phleum pratense*, *Tri p*: *Trifolium pratense*, *Alo*: *Alopecurus pratensis*, *Dac*: *Dactylis glomerata*, *Ger*: *Geranium pratense*, *Poa*: *Poa trivialis*, *Tri r*: *Trifolium repens*.

Block	Plot	Composition code	Species richness	Legume presence	*Ant*	*Arr*	*Phl*	*Tri p*	*Alo*	*Dac*	*Ger*	*Poa*	*Tri r*	Host plant biomass
2	86	S01M21	1		1									499.8
4	62	S01M21	1		1									356.7
3	57	S01M22	1			1								384.7
4	48	S01M22	1			1								374.2
2	8	S01M44	1				1							326.95
3	11	S01M44	1				1							199.65
2	20	S01M60	1	1				1						505.25
4	24	S02M18	2			1			1					101.35
1	92	S02M19	2		1	1								314.9
1	9	S02M24	2		1						1			37.105
4	54	S02M25	2			1					1			234.25
2	63	S02M27	2				1		1					48.55
3	9	S02M28	2		1		1							476.15
2	19	S02M29	2			1	1							680.95
3	33	S02M31	2				1				1			137.2
1	12	S02M37	2				1					1		406.3
4	2	S02M38	2	1				1	1					23.4
3	1	S02M39	2	1	1			1						858.15
1	39	S02M40	2	1		1		1						631.45
4	32	S02M41	2	1				1		1				32.155
3	28	S02M42	2	1				1			1			116.3
2	82	S02M43	2	1			1	1						513.1
2	69	S02M44	2	1				1				1		165.6
2	18	S02M46	2	1	1								1	309.15
2	25	S02M47	2	1		1							1	394.35
4	19	S02M50	2	1			1						1	273.3
3	75	S03M05	3			1	1				1			399.6
4	56	S03M13	3	1	1			1			1			290.785
1	41	S03M15	3	1		1	1	1						743.25
4	50	S03M15	3	1		1	1	1						271.45
4	35	S03M16	3	1	1			1				1		556.95
2	46	S03M20	3	1	1						1		1	435.85
4	43	S03M21	3	1			1				1		1	359.3
1	17	S04M20	4		1	1	1					1		379
1	54	S04M23	4	1	1	1		1			1			432.45
2	67	S04M23	4	1	1	1		1			1			248.9
2	91	S04M26	4	1			1	1			1	1		409.85
4	78	S04M27	4	1	1	1					1		1	271.25
4	36	S04M29	4	1	1				1			1	1	33.4
3	19	S04M34	4	1	1		1	1					1	364.65
2	64	S06M03	6	1		1	1	1	1	1		1		267.2
1	3	S06M06	6	1	1	1	1		1			1	1	248.85
1	11	S06M07	6	1	1		1			1	1	1	1	32.58
4	64	S06M08	6	1	1	1		1	1		1		1	178.67
2	2	S09M01	9	1	1	1	1	1	1	1	1	1	1	134.695
3	91	S09M01	9	1	1	1	1	1	1	1	1	1	1	153.15
4	12	S09M01	9	1	1	1	1	1	1	1	1	1	1	142.55
Total			**47**	**30**	**22**	**21**	**22**	**21**	**10**	**6**	**17**	**12**	**14**	

Table S2: List of all species in plant–aphid–parasitoid food webs, sorted by trophic level, with average densities across all plots (biomass in g per m^2 for plants, individuals per m^2 for aphids and parasitoids, sums over all sampling dates). Because mummy parasitoids attack primary parasitoids and hyperparasitoids (Müller *et al.*, 1999) they can be considered a slightly higher trophic level than hyperparasitoids, i.e level 4–5 in our food webs. Nomenclature follows Rothmaler (2002) for plant species and Stresemann (1994) for aphid species. Authorities for parasitoids are given in brackets following species names. Provisional species names are used for three undescribed *Alloxysta* species (F. van Veen, pers. comm.). Two rare aphid species and one rare mummy parasitoid species could not be identified and were assigned to morphospecies.

Trophic level	Group	Species	Density	Number in Fig. 8
1	Plant	*Anthriscus silvestris*	83.8	1
1	Plant	*Phleum pratense*	79.9	2
1	Plant	*Trifolium pratense*	42.6	3
1	Plant	*Arrhenatherum elatius*	107.6	4
2	Aphid	*Aphis fabae*	12.65	10
2	Aphid	*Cavariella aegopodii*	149.44	11
2	Aphid	*Dysaphis anthrisci*	0.60	12
2	Aphid	*unidentified species 1*	0.04	13
2	Aphid	*unidentified species 2*	0.71	14
2	Aphid	*Diuraphis muehlei*	251.77	15
2	Aphid	*Schizaphis graminum*	4.63	16
2	Aphid	*Sipha maydis*	79.46	17
2	Aphid	*Aphis scaliai*	24.89	18
2	Aphid	*Therioaphis trifolii*	21.95	19
3	Primary parasitoid	*Adialytus arvicola* (Starý)	3.26	20
3	Primary parasitoid	*Aphelinus asychis* (Walker)	1.79	21
3	Primary parasitoid	*Aphelinus flaviventris* (Kurdjumov)	0.08	22
3	Primary parasitoid	*Aphelinus varipes* (Förster)	0.40	23
3	Primary parasitoid	*Aphidius salicis* (Haliday)	2.64	24
3	Primary parasitoid	*Lysiphlebus fabarum* (Marshall)	0.53	25
3	Primary parasitoid	*Praon exoletum* (Nees)	0.03	26
3	Primary parasitoid	*Trioxys brevicornis* (Haliday)	4.19	27
4	Hyper parasitoid	*Alloxysta brachyptera* (Hartig)	0.285	30
4	Hyper parasitoid	*Alloxysta circumscripta* (Hartig)	0.005	31
4	Hyper parasitoid	*Alloxysta "fl3"*	0.282	32
4	Hyper parasitoid	*Alloxysta "new"*	0.096	33
4	Hyper parasitoid	*Alloxysta "o2"*	0.087	34
4	Hyper parasitoid	*Alloxysta victrix* (Westwood)	0.106	35
4	Hyper parasitoid	*Phaenoglyphis villosa* (Hartig)	0.090	36
4 (5)	Mummy parasitoid	*Asaphes suspensus* (Nees)	0.841	37
4 (5)	Mummy parasitoid	*Asaphes vulgaris* (Walker)	0.721	38
4 (5)	Mummy parasitoid	*Coruna clavata* (Walker)	0.979	39
4 (5)	Mummy parasitoid	*Dendrocerus aphidum* (Rondani)	0.861	40
4 (5)	Mummy parasitoid	*Dendrocerus carpenteri* (Curtis)	1.989	41
4 (5)	Mummy parasitoid	*Syrphophagus aphidivorus* (Mayr)	0.050	42
4 (5)	Mummy parasitoid	unidentified Chalcidoidea	0.010	43

CHAPTER 5

Plant species loss affects life-history traits of aphids and their parasitoids

Petermann JS, Müller CB, Roscher C, Weigelt A, Weisser WW, Schmid B, Manuscript

"*In one case, mating was observed on a tomato.*"
(Visser, 1994)

"*Überholen uns die Insekten?*"
(Fischli & Weiss, 2007)

Abstract

The consequences of plant species loss are rarely assessed in a multi-trophic context and especially effects on life-history traits of higher trophic levels have remained largely unstudied. We used a grassland biodiversity experiment to test if demographic characteristics of aphids and their parasitoids were affected by manipulations of plant diversity. As components of plant diversity we considered the quantitative effects of species richness and the qualitative effects of the presence of nitrogen-fixing legumes on higher trophic levels. We found that the proportion of winged aphid morphs decreased with increasing plant species richness which was correlated with decreasing individual host plant biomass. Similarly, emergence proportions of parasitoids decreased with increasing plant species richness and both, emergence proportions and proportions of female parasitoids were lower in plots with legumes where host plants had increased nitrogen concentrations. This could be taken as an indication that aphids were better defended against parasitoids in high-nitrogen environments. Body weights of emerged individuals of the two most abundant parasitoids were, however, higher in plots with legumes, suggesting that once parasitoids could overcome aphid defences, they could profit from larger or more nutritious hosts. Our study demonstrates that cascading effects of plant species loss on higher trophic levels such as aphids and their parasitoids begin with changed life-history traits of these insects. Thus, life-history traits of organisms at higher trophic levels may be useful indicators of bottom-up effects of plant diversity on the biodiversity of secondary producers.

Introduction

The consequences of the prominent loss of species have been studied extensively, but rarely across several trophic levels (Balvanera et al. 2006, Duffy et al. 2007). However, if plants as primary producers are lost from the system, bottom-up cascades (Hunter and Price 1992) could lead to direct and indirect effects on other trophic levels. The first bottom-up cascades were described from aquatic systems, but they can be similarly strong in terrestrial systems (reviewed by Kagata and Ohgushi 2006). Indeed, field and laboratory experiments have demonstrated terrestrial community- and population-level bottom-up cascades, i.e. effects of plant abundance or richness on the abundance or richness of herbivores and predators (Chapter 4, see also e.g. Siemann et al. 1998, Knops et al. 1999, Haddad et al. 2001, Dyer and Stireman 2003, Gange et al. 2003, Aquilino et al. 2005).

In contrast, individual-level bottom-up cascades affect life-history variables of individuals at higher trophic levels (Kagata and Ohgushi 2006). Studies focussing on this type

of cascade most often manipulate plant quality instead of plant abundance or richness (e.g. Harvey et al. 2003, Wurst and Jones 2003, Soler et al. 2005, de Sassi et al. 2006, Härri et al. 2008a, b). The different types of cascade have hardly ever been studied simultaneously (Kagata and Ohgushi 2006, but see Omacini et al. 2001, Bezemer et al. 2005, Bukovinszky et al. 2008). Here, we link community- with individual-level cascades, using aphids and their parasitoids as a model system, and hypothesise that changes in plant community diversity cause cascading effects on life-history traits of individuals at higher trophic levels.

Previous research has demonstrated that plant diversity influences plant biomass production and plant nutrient contents (e.g. reviewed by Hooper et al. 2005, Balvanera et al. 2006). More specifically, biomass of individual species may decline, increase or vary independently with increasing plant species richness while community biomass commonly increases (Hooper et al. 2005). Furthermore, the presence of nitrogen-fixing legumes in the plant community has been found to increase community biomass (e.g. Spehn et al. 2002), aboveground plant nitrogen pools (Spehn et al. 2002, Roscher et al. 2008) and plant tissue nitrogen concentration (Temperton et al. 2007).

In turn, demographic characteristics of plant-associated insects have been shown to respond to changes in host plant biomass and host plant quality, sometimes even several trophic levels above plants (Price 1997, Lill and Marquis 2001, Teder and Tammaru 2002, Harvey et al. 2003, Wurst and Jones 2003, Soler et al. 2005, de Sassi et al. 2006, Bukovinszky et al. 2008, Härri et al. 2008a, b). An important aspect of host plant quality is their nitrogen concentration because insects are generally nitrogen-limited (Lawton and McNeill 1979, White 1984, Davidson and Potter 1995). Therefore, we expect demographic characteristics of aphid herbivores and their parasitoids to be affected by changes in plant species richness and legume presence, mediated by changes in host plant biomass and nitrogen concentration. The potentially altered life-histories may then explain the previously described community-level cascades of plant diversity on aphid and parasitoid richness and abundance (Chapter 4).

Our model system, the plant–aphid–parasitoid food web is ideally suited to study these bottom-up cascades because it allows the establishment of direct individual-based links that are fully quantifiable at each level (Müller et al. 1999). Aphids are specialised herbivores which often prefer single or few host plant species at least during part of their life cycle (Dixon 1998). Once a winged (alate) aphid coloniser has reached such a host plant a colony forms via asexual reproduction of non-winged (apterous) individuals which remain rather immobile on the same plant individual. Parasitic wasps parasitize aphids by laying single eggs into their body (Völkl et al. 2007). The parasitoid larva feeds internally until the aphid dies

and forms a hard-shelled "mummy" in which the parasitoid larva pupates. The adult primary parasitoid emerges from the mummy shortly after, unless it is itself parasitized by a secondary parasitoid. Adult female parasitods prefer to oviposit in high-quality hosts (Kidd and Jervis 1991), sometimes using lower-quality hosts as food source for themselves. They furthermore supplement their diet with aphid honeydew (Wyckhuys et al. 2008) and floral resources (e.g. Araj et al. 2008).

To test the hypothesis that plant diversity affects life-history variables of organisms at higher trophic levels we recorded four demographic traits of aphids and their parasitoids. These traits were the proportion of winged individuals in aphid colonies, the emergence proportion of parasitoids, the proportion of parasitoids that are female and the body weight of the two most abundant parasitoids. Wings are obviously costly for aphids (Dixon 1998, Müller et al. 2001) and are therefore not constantly expressed. The production of winged morphs in aphids has been suggested to serve two main purposes besides the obligatory change of host plant species in the life cycles of some species: firstly, the avoidance of deteriorating nutritional conditions and secondly, the escape from predators (Sutherland 1967, Weisser et al. 1999, Müller et al. 2001, Sloggett and Weisser 2002). Thus, the proportion of winged aphids in a colony may reflect its nutritional or enemy environment which we anticipate to change with changing plant diversity.

Whether a parasitoid larvae develops and emerges successfully from the aphid mummy as an adult depends amongst other things on aphid quality (Ashouri et al. 2001) and the aphid's resistance (Ferrari et al. 2001, Li et al. 2002). To improve this defence, aphids and other herbivores are able to use compounds produced by the host plant or a host plant symbiont such as an endophytic fungus (Barbosa et al. 1991, Francis et al. 2001). By preventing the parasitoid from emerging, the host aphid may not save its own life but at least avert the attack on genetically identical individuals. Therefore, if changes in the plant community affect the aphids` quality in terms of nutritional value, size or defensive abilities, these changes are expected to influence the proportion of successfully emerging parasitoids.

Parasitoid body weight is generally correlated with fitness (Godfray 1994, Visser 1994) which has been shown to be controlled by host nutritional quality and especially by host size (e.g. Sequeira and Mackauer 1992, Bukovinszky et al. 2008). Furthermore, some hymenopteran parasitoids are able to select the sex of their offspring at oviposition: fertilised eggs develop into females, unfertilised ones into males (Godfray 1994). Because female parasitoids gain more from being large (Charnov et al. 1981, Ueno 1999), female eggs are

typically laid into the highest-quality hosts (Charnov et al. 1981). Thus, heavier parasitoids with a female-biased sex ratio could be expected to emerge in favourable environments.

In this study, we measured demographic variables of aphids and parasitoids in experimental grassland communities varying in plant species richness and legume presence to test the hypotheses that (1) plant species loss has bottom-up cascading effects on life-history traits of organisms at higher trophic levels, (2) these cascades are mediated by diversity-related changes in host plant biomass and host plant nitrogen content, (3) compositional effects of plant diversity, e.g. the presence of legumes, have especially strong effects on insect life-history parameters.

Methods

Experimental design

This study was conducted as part of the Jena Experiment, a temperate grassland biodiversity experiment in Jena, Germany (Roscher et al. 2004). The experimental site is a floodplain area close to the river Saale which was used for agricultural cropping before the experiment started in 2002. The site has not received fertiliser since then and is mown twice per year, a typical mowing regime of these grasslands. In the 3.5 x 3.5 m plots that were used for this study, nine dominant plant species from semi-natural, mesophilic grasslands were sown in 2002 as monocultures and mixtures (richness levels of 1, 2, 3, 4, 6, and 9 species, Roscher et al. 2005). The original species compositions were maintained by weeding at regular intervals (Roscher et al. 2004). The plots were arranged in four blocks with increasing distance to the river. Preliminary surveys showed that aphid could be regularly found on four of the nine species at the field site (*Anthriscus sylvestris, Arrhenatherum elatius*, *Phleum pratense* and *Trifolium pratense,* Table 1). Only plots containing at least one of these host plant species were hence used for this study (Table 2).

Data collection

We identified and counted all aphids (a total of > 16,000 individuals), including nymphs and winged morphs in the same 0.2 x 3 m transect across the middle of the plots four times from May (first appearance of aphids at the field site) to August 2006 (almost no aphids found after the fourth sampling period). All sampling campaigns were completed within about one week, two before the first mowing of the field site (around 2 June and 17 June) and two between the first and the second mowing (20 July and 2 August). Sampling was usually done in the

mornings from a bench across the plots to avoid disturbing the vegetation and the aphid populations.

All parasitized aphids (mummies) in the transects were collected during the sampling periods. Additionally, all mummies in a surrounding plot area (usually 4 m^2) were collected at the same time to be able to detect the full parasitoid community of a plot. A total of more than 3,500 mummies was collected, about one third of them from the transects. Empty mummies were also collected but not used in any analysis. All mummies were placed individually in gelatine capsules in the field and taken to the laboratory for rearing of the parasitoids. To induce parasitoid emergence, all mummies remaining after four months were subjected to a 3-month cold-warm-cold cycle with a minimum of 4°C. A total of about 2,000 parasitoids (about 1,700 primary parasitoids and 300 secondary parasitoids) emerged and were identified to species level. We individually weighed all 1,072 emerged individuals of the two most abundant parasitoid species (both primary parasitoids) on a microbalance (Mettler Toledo MX5) to the nearest microgram after drying at 70 °C for two days. These were *Adialytus arvicola*, predominantly parasitizing the aphid *Sipha maydis* on the host plant *A. elatius*; and *Trioxys brevicornis*, predominantly parasitizing the aphid *Cavariella aegopodii* on the host plant *A. sylvestris* (Table 1).

The biomass of aphid host plants was determined by clipping the vegetation at a height of 3 cm in two 20 x 50 cm areas within each plot in May and August 2006. The harvested biomass was sorted into species, dried at 70 °C for 48 h and weighed. The biomass data from the two harvests were averaged over the two sampling quadrates and summed up over the whole year. Nitrogen concentrations of aphid host plants were measured for each plant species from biomass samples harvested in May 2004 (Roscher et al. 2008) in the same plots that were used for aphid counts or in replicate plots with the same plant composition.

Data analysis

The proportion of winged aphid morphs was calculated by dividing the density of winged individuals by the total density of the respective aphid species. Alatiform nymphs were rarely encountered and included as non-winged morphs; parasitized aphids were excluded. Three outliers with very low population densities and unusually high proportions of winged morphs (> 0.38) were excluded. The proportion of emerged parasitoids (including both primary and secondary parasitoids) was calculated as the number of emerged parasitoids divided by the sum of emerged parasitoids and remaining mummies of each aphid species. The proportion of female emerged parasitoids was calculated for each species by dividing the density of female

individuals of a parasitoid species (again primary and secondary parasitoids) by the total density of emerged individuals of this species. Proportions of 0 and 1 were again excluded both for the proportion of emerged parasitoids and the proportion of female parasitoids because they usually only occurred with very low parasitoid densities. One parasitoid species, *Lysiphlebus fabarum* which parasitized the aphid *Aphis scaliai* on the legume *T. pratense*, reproduces predominantly asexually in Europe (Belshaw et al. 1999) and was also excluded from this analysis. These exclusion criteria led to the elimination of all parasitoids that emerged from aphids with legume host plants from the analysis of female proportions. Parasitoid body weight was measured for two parasitoid species which only parasitized aphids with non-legume host plants. The proportion of winged aphid individuals and the proportion of emerged parasitoids were calculated on the level of aphid species in each plot (in the latter case because parasitoids that failed to emerge could not be identified). The proportion of female parasitoids and mean parasitoid body weight were calculated on the level of the parasitoid species in each plot. All data were aggregated over the four census times.

We used multiple regression and analysis of variance (ANOVA) to analyse the data. The response variables were not transformed because model checking procedures indicated that this was not necessary and analyses with transformed variables gave similar results. The biomass of aphid host plants (in g/m^2) and their nitrogen concentration (in %) were used as covariables. All analyses were carried out with the statistical software R, version 2.7.2 (R Development Core Team, http://www.r-project.org).

Results

Plant-related variables

The biomass of the four host plant species declined with increasing plant species richness (Table 3). Host plant nitrogen concentration slightly increased with increasing plant species richness and was higher in legume (2.3 ± 0.8 %) than in non-legume plots (1.4 ± 0.3%) and higher for legume (*T. pratense*: 2.9 ± 0.5 %) than for non-legume host plants (*A. sylvestris*: 2.0 ± 0.4 %, *A. elatius*: 1.2 ± 0.3 %, *P. pratense*: 1.3 ± 0.3 %). The total biomass of the host plant species on which mummies of the two most abundant parasitoid species (*Adialytus arvicola* and *Trioxys brevicornis,* Table 1) were found also decreased with increasing plant species richness ($F_{1,24} = 16.6$, $P < 0.001$) and was higher in plots containing legumes (452 ± 246 g/m^2) than in plots from which legumes were absent (198 ± 123 g/m^2, $F_{1,24} = 34.7$, $P < 0.001$). However, their nitrogen concentration did not significantly increase with plant species richness ($F_{1,18} = 1.15$, $P = 0.297$).

Proportion of winged aphids

Winged individuals were found only in colonies of four out of the ten aphid species: *Aphis fabae*, *Cavariella aegopodi* (both mainly on the host plant *A. sylvestris*), *Diuraphis muehlei* on the host plant *P. pratense*) and *Sipha maydis* (on the host plant *A. elatius*). The proportion of winged morphs declined with increasing plant species richness, both for these four aphid species (Fig. 1) and when including all aphid species (Table 4). The biomass of the aphid host plants explained part of this effect (see "% SS" in Table 4): higher host plant biomass had an increasing effect on the proportion of winged aphids, but since host plant biomass declined with plant species richness, the proportion of winged individuals declined as well. Neither aphid density nor aphid load (aphid density per host plant biomass) nor parasitoid density had significant effects on the proportions of winged aphids (results not shown).

Parasitoid emergence proportion

The proportion of emerged parasitoids declined with increasing plant species richness and was lower in plots containing legumes (Fig. 2, Table 5). Parasitoids of aphid species with legume hosts showed very low emergence proportions, but legume presence also had a negative effect on the emergence proportions of parasitoids of aphid species with non-legume hosts (Fig. 2). Host plant biomass had a significant positive and host plant nitrogen concentration a significant negative effect on emergence proportions (Table 5). Emergence proportions were similar in legume and non-legume plots for the two most abundant parasitoids, *A. arvicola* and *T. brevicornis*, whose mummies were only found on non-legume host plants (results not shown).

Proportion of female parasitoids

The proportion of female parasitoids was independent of plant species richness but was lower with legume presence (Fig. 3, Table 6). Host plant biomass and nitrogen concentration had significant negative effects on the proportion of female parasitoids and explained part of the negative legume effect (Table 6). Because only parasitoids emerging from mummies on non-legume host plants were considered, the negative effect of legumes on the proportion of females was mediated via increased nitrogen concentrations of non-legume host plants in the presence of legumes. However, the legume effect was not significant for the two most abundant parasitoids, *A. arvicola* and *T. brevicornis* (results not shown).

Parasitoid body weight

The body weight of the two most abundant parasitoids, *A. arvicola* and *T. brevicornis* was similar across all plant species richness levels but was higher in the presence of legumes for both parasitoid species (Fig. 4, Table 7). Because both species emerged only from mummies on non-legume host plants, these effects were again indirect: They were largely due to increased biomass and nitrogen concentration of these non-legume host plants in plots containing legumes (Table 7).

Discussion

Our results demonstrate that plant species richness and the presence of legumes in plant communities affect the life history of aphids and their parasitoids both directly and indirectly via host plant biomass and nitrogen concentration. This is consistent with community-level cascading effects of plant species richness on species richness and densities of aphids and their parasitoids that were found in a parallel study (Chapter 4).

Proportion of winged aphids

The proportion of winged aphids decreased with increasing plant species richness, largely as a result of a simultaneous decrease in aphid host plant biomass. Whereas low host plant abundance typically has a negative effect on herbivore densities (Chapter 4, Knops et al. 1999, Haddad et al. 2001, Otway et al. 2005), the proportion of winged individuals was expected to rise with resource limitation since wing production is a strategy to escape deteriorating conditions by dispersing (Sutherland 1967, Müller et al. 2001). The absence of a shift toward dispersal morphs was consistent with the observation that aphid load (aphid density per host plant biomass) did not affect the proportion of winged morphs. Thus there was no indication of a crowding effect in high plant species richness. Müller et al. (2001) suggested that natural densities of aphids are rarely high enough to induce wing production as a response to crowding. Host plant nitrogen concentration and parasitoid density did not affect the proportion of winged morphs, implying that plant quality in terms of nitrogen content and natural enemy abundance (at least regarding parasitoids) are rather unlikely explanations for the negative plant species richness effect on the production of winged morphs.

Because a substantial cost is associated with wing production (Dixon 1998, Müller et al. 2001) another study concluded that resources might sometimes be too low to induce wing production at all, especially if predator pressure is low (Züst et al. 2008). So the resource-limitation argument could be reversed to explain the extremely low proportions of winged

aphids in communities with high plant species richness and low host plant biomass. However, we found relevant proportions of winged individuals only in three aphid species and it has been shown that intra- and interspecific variation in wing induction can be very large (Müller et al. 2001). Furthermore, other abiotic effects that we did not measure, e.g. temperature, may be important triggers (Müller et al. 2001), cautioning against strong conclusions from our results.

Parasitoid emergence proportion

Emergence proportions of parasitoids similarly decreased with increasing plant species richness and were lower in plant communities containing legumes than in legume-free communities. These effects were partially explained by a positive effect of host plant biomass (which decreased with plant species richness) and a negative effect of host plant nitrogen concentration on emergence success. Plant nitrogen concentrations, which are often increased even in non-legumes by the presence of nitrogen-fixing legumes (Temperton et al. 2007), can have positive or negative effects on higher trophic levels. On the one hand, plants with higher nitrogen contents may be more nutritious for herbivores who are generally nitrogen-limited (Lawton and McNeill 1979, White 1984, Davidson and Potter 1995, Kempel et al. 2009).

On the other hand, nutrient availability is known to affect plant allocation to secondary metabolites (Bryant et al. 1983, Herms and Mattson 1992) and plants may use surplus nitrogen to produce higher levels of nitrogen-based defence compounds (e.g. Mattson 1980, Lyons et al. 1986). These opposing effects may explain why fertiliser effects on herbivores can sometimes not be detected (Müller et al. 2005).

One trophic level above herbivores, the same dichotomy may become apparent. Natural enemies of herbivores are even more strongly limited by nitrogen (Mayntz and Toft 2001, Fagan et al. 2002) and might do better on nitrogen-rich hosts. However, some herbivores can use nitrogen-based plant compounds or simply their own high nutritional status on nitrogen-rich host plants to mount defences against predators and parasitoids (Barbosa et al. 1991, Francis et al. 2001). The latter seems to operate in our case with parasitoid emergence success potentially being lower on nitrogen-rich host plants due to increased aphid defences. We might even have underestimated parasitoid mortality in our study because parasitoid larvae that were killed and absorbed by the aphid metabolism at an early stage could not be detected. These results may in part explain the decrease in parasitoid densities and richness with increasing plant species richness that we found in a parallel study (Chapter 4).

Proportion of female parasitoids

For all parasitoid species combined, the proportion of female individuals decreased with legumes being present in the plant community. A large part of this effect was explained by the indirect nitrogen-enrichment of non-legume host plants in the presence of legumes. Since mated parasitoid females can determine the sex of their offspring at oviposition (Godfray 1994), they might have sensed augmented aphid defences on high-nitrogen host plants and avoided "wasting" females on risky hosts. On the other hand, the parasitoid sexes might have differential mortality (Godfray 1994), with female larvae more prone to abortion as a result of aphid defences, potentially explaining the lower emergence rates in legume plots.

Parasitoid body weight

In contrast, the body weight of the two most abundant primary parasitoids, *A. arvicola* and *T. brevicornis*, increased with the presence of legumes in the plant community. Host plant nitrogen concentration (and host plant biomass) had a positive effect in this case. Since we did not find a negative effect of legume presence on the emergence proportion or the proportion of females in these two species, we conclude that they might be resistant to potentially increased aphid defences in legume plots. This resistance may even explain their high abundance at out field site. These two species seemed to instead profit from the presence of legumes. We did not measure aphid body weight or nitrogen concentration and hence have no conclusive evidence for either higher nitrogen concentrations of hosts (Mayntz and Toft 2001, Fagan et al. 2002, Hunter 2003) or larger host sizes indeed mediating higher parasitoid body weights in communities with legumes. Another field experiment found a higher body mass gain of herbivores, in this case grasshoppers, in legume-containing plant communities (Pfisterer et al. 2003). Since host size is typically strongly correlated with parasitoid size (Cohen et al. 2005), a size-mediated effect seems plausible.

Conclusions

We found profound effects of plant species richness and community composition cascading up the food web to affect aphid and parasitoid life-history traits. A particularly strong effect was exerted by legumes. This plant functional group had an impact up to the third trophic level in the food web, sometimes even mediated via an additional interaction at the plant level, thus affecting even food webs on non-legume host plants.

In contrast, a parallel study found only plant species richness effects but no effects of legume presence on aphid and parasitoid richness and densities (Chapter 4), underlining the importance of demographic studies to detect different pathways of effects of plant species loss on associated biodiversity. This difference in the effect of legume presence between the two studies may indicate that cascading bottom-up effects on insect demographies are more strongly resource quality-mediated, whereas cascading effects on insect species richness and density seem to be rather abundance- and richness-mediated. On the other hand, it is possible, that insect life-history studies detect effects of plant species loss at an earlier stage than richness or abundance studies. Similar observations have been made in analyses of vegetation responses to habitat change, where demographic changes could be used as early indicators (Buhler and Schmid 2001).

The altered life-histories are expected to eventually result in altered species abundances and richness. One example for this link in our data is the low suitability of species-rich plant communities for parasitoids. In the present study, we found lower emergence rates and female proportions, potentially due to increased aphid defences. These are paralleled by low parasitoid densities and species richness (Chapter 4), possibly a result of reduced parasitoid reproduction. We therefore advocate the simultaneous study of individual-level cascades to predict and explain population- and community-level cascades of plant species loss on food webs.

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Figures

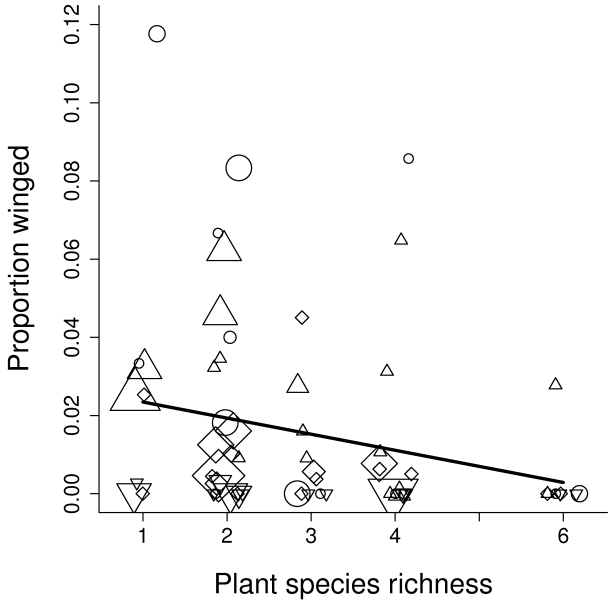

Fig. 1: The proportion of winged aphids (winged individuals per total individuals) as a function of plant species richness. Only four aphid species: *A. fabae* (circles), *C. aegopodi* (up-facing triangles, both species mainly on the host plant species *A. sylvestris*) and *D. muehlei* (diamonds, on the host plant species *P. pratense*) and *S. maydis* (down-facing triangles, on the host plant species *A. elatius*) ever produced winged morphs and are shown.

The size of the plotting symbol is proportional to the biomass (g/m^2) of the host plant of the respective aphid species in the respective plot. Host plant biomass below $200g/m^2$ is represented by a symbol with a fixed size.

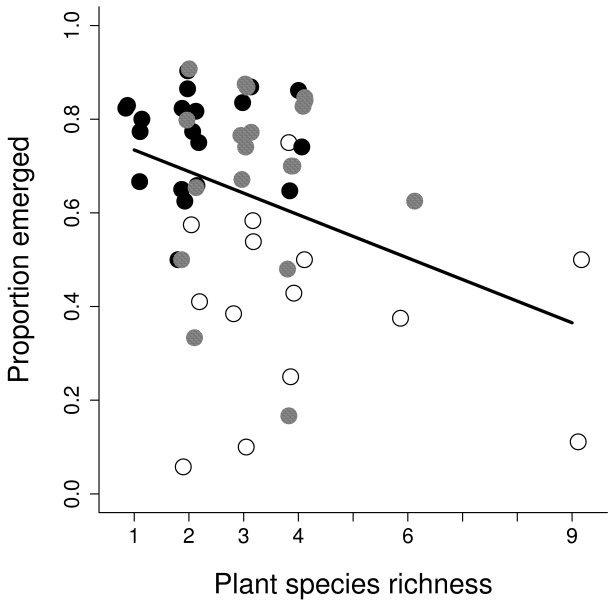

Fig. 2: The proportion of emerged parasitoids (emerged individuals per total mummies) as a function of plant species richness. Closed black symbols depict parasitoids emerged from mummies on non-legume host plants (*A. sylvestris*, *A. elatius*, *P. pratense*) in non-legume plots, grey symbols parasitoids emerged from mummies on those non-legume host plant species in legume plots and open symbols parasitoids emerged from mummies on a legume host plant (*T. pratense*). The regression line was fitted to all data points.

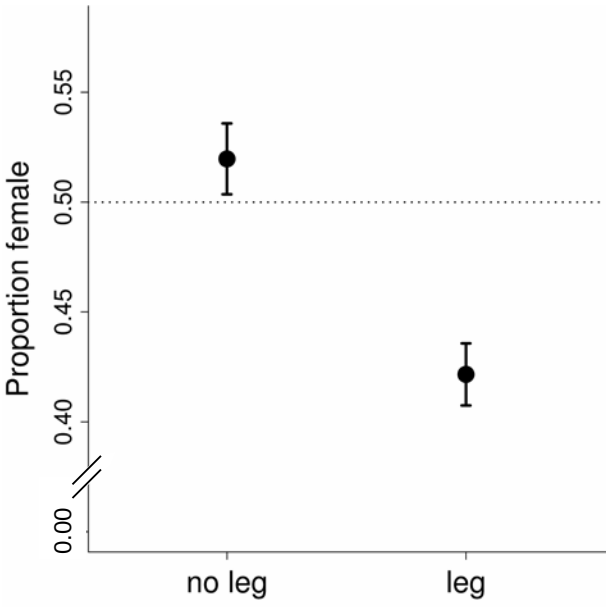

Fig. 3: The proportion of female parasitoids ± standard error (female parasitoids per total parasitoids) in plots without legumes ("no leg") and with legumes ("leg"). Only parasitoids emerged from mummies on non-legume host plants (*A. sylvestris, A. elatius, P. pratense*) were included. The dotted line shows the 1:1 sex ratio.

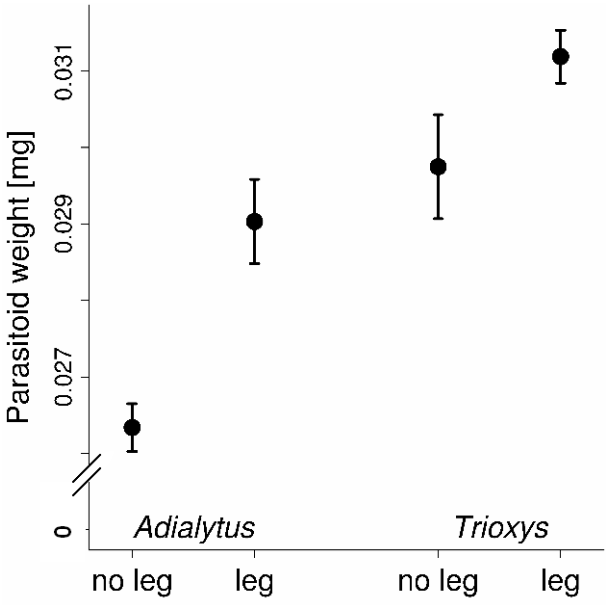

Fig. 4: Body weight ± standard error (mg) of the two most abundant primary parasitoids *Adialytus arvicola* and *Trioxys brevicornis* in plots without legumes ("no leg") and with legumes ("leg"). Both parasitoid species developed only in aphids from non-legume host plant species (*A. elatius, A. sylvestris*, respectively).

Tables

Table 1 (following page): List of all species with average densities (biomass in g per m^2 for plants, individuals per m^2 for aphids and parasitoids, sums over all sampling dates), proportions of winged aphids (excluding three outliers, see Methods), proportions of emerged parasitoids (excl. proportions of 0 and 1, see Methods), proportions of female parasitoids (excl. proportions of 0 and 1, see Methods) and parasitoid body weights (in mg) across all respective plots. Plant nomenclature follows Rothmaler (2002), aphid nomenclature follows Stresemann (1994). Authorities for parasitoids are given in parentheses behind species names. Two rare aphid species and one rare parasitoid species could not be identified due to the lack of material and were assigned to morphospecies. Three species of *Alloxysta* have not been described and were given provisional names (Frank van Veen, personal communication). Families: Ah: Aphididae, Al: Aphelinidae, Ap: Apiaceae, Br: Braconidae, Ch: Chaitophoridae, En: Encyrtidae, Fa: Fabaceae, Fi: Figitidae, Me: Megaspilidae, Po: Poaceae, Pt: Pteromalidae, hosts: *Ant*: *Anthriscus sylvestris*, *Aph: Aphis scaliai, Arr*: *Arrhenatherum elatius*, *Cav: Cavariella aegopodii*, *Diu: Diuraphis muehlei, Phl*: *Phleum pratense, Sch: Schizaphis graminum, Sip: Sipha maydis, The: Therioaphis trifolii, Tri p*: *Trifolium pratense*.

Group	Species	Family	Host	Density	Winged	Emerged	Females	Weight
Plant	*Anthriscus silvestris*	Ap		83.8 ± 25.7				
Plant	*Arrhenaterum elatius*	Po		107.6 ± 22.5				
Plant	*Phleum pratense*	Po		79.9 ± 19.3				
Plant	*Trifolium pratense*	Fa		42.6 ± 13.3				
Aphid	*Aphis fabae*	Ah	*Ant, Tri p*	12.65 ± 3.96	0.0297 ± 0.00460	excl.		
Aphid	*Aphis scaliai*	Ah	*Tri p*	24.89 ± 8.77	0	0.340 ± 0.067		
Aphid	*Cavariella aegopodii*	Ah	*Ant*	149.44 ± 42.61	0.0252 ± 0.0043	0.699 ± 0.063		
Aphid	*Diuraphis muehlei*	Ah	*Phl*	251.77± 72.52	0.0083 ± 0.0043	0.740 ± 0.067		
Aphid	*Dysaphis anthrisci*	Ah	*Ant*	0.60 ± 0.60	0	excl.		
Aphid	*Schizaphis graminum*	Ah	*Phl*	4.63 ± 2.98	0	excl.		
Aphid	*Sipha maydis*	Ch	*Arr, Phl, Tri p*	79.46 ± 25.60	0.0003 ± 0.0043	0.744 ± 0.073		
Aphid	*Therioaphis trifolii*	Ah	*Tri p*	21.95 ± 4.92	0	0.500 ± 0.242		
Aphid	unidentified species 1		*Ant*	0.04 ± 0.04	0	excl.		
Aphid	unidentified species 2		*Ant*	0.71 ± 0.71	0	excl.		
Primary	*Adialytus arvicola* (Starý)	Br	*Sip*	3.26 ± 1.44			0.544 ± 0.041	0.0270 ± 0.0003
Primary	*Aphelinus asychis* (Walker)	Al	*Diu, Sch*	1.79 ± 0.53			0.474 ± 0.038	
Primary	*Aphelinus flaviventris* (Kurdjumov)	Al	*Sch*	0.08 ± 0.08			0.647 ± 0.137	
Primary	*Aphelinus varipes* (Förster)	Al	*Diu*	0.40 ± 0.18			0.511 ± 0.056	
Primary	*Aphidius salicis* (Haliday)	Br	*Cav*	24.89 ± 8.77			0.523 ± 0.038	
Primary	*Lysiphlebus fabarum* (Marshall)	Br	*Sip, Aph*	0.53 ± 0.22			excl.	
Primary	*Praon exoletum* (Nees)	Br	*The*	0.03 ± 0.01			excl.	
Primary	*Trioxys brevicornis* (Haliday)	Br	*Cav*	4.19 ± 1.56			0.408 ± 0.034	0.0309 ± 0.0003
Secondary	*Alloxysta* "fl3"	Fi	*Cav*	0.282 ± 0.150			0.286 ± 0.137	
Secondary	*Alloxysta* "new"	Fi	*Diu*	0.096 ± 0.042			0.458 ± 0.097	
Secondary	*Alloxysta* "o2"	Fi	*Cav*	0.087 ± 0.053			excl.	
Secondary	*Alloxysta brachyptera* (Hartig)	Fi	*Diu, Sip*	0.285 ± 0.194			0.619 ± 0.097	
Secondary	*Alloxysta circumscripta* (Hartig)	Fi	*The*	0.005 ± 0.005			excl.	
Secondary	*Alloxysta victrix* (Westwood)	Fi	*Cav*	0.106 ± 0.079			0.500 ± 0.137	
Secondary	*Asaphes suspensus* (Nees)	Pt	*Diu, Cav*	0.841 ± 0.329			0.397 ± 0.061	
Secondary	*Asaphes vulgaris* (Walker)	Pt	*Cav*	0.721 ± 0.431			0.156 ± 0.097	
Secondary	*Coruna clavata* (Walker)	Pt	*Cav*	0.979 ± 0.721			excl.	
Secondary	*Dendrocerus aphidum* (Rondani)	Me	*Cav*	0.861 ± 0.603			0.575 ± 0.068	
Secondary	*Dendrocerus carpenteri* (Curtis)	Me	*Cav, Sip*	1.989 ± 0.667			0.437 ± 0.043	
Secondary	*Phaenoglyphis villosa* (Hartig)	Fi	*Cav*	0.090 ± 0.065			excl.	
Secondary	*Syrphophagus aphidivorus* (Mayr)	En	*Diu, Cav*	0.050 ± 0.037			excl.	
Secondary	unidentified Chalcidoidea		*Diu, Aph*	0.010 ± 0.007			excl.	

Table 2 (following page): List of all 47 sampled plots with their block number, plot number, composition code, plant species richness, the presence of legumes, the presence of the nine plant species in the plant assemblage and the total host plant biomass (sum across all host plant species and both harvests in 2006). In some cases, replicate plots with the same plant composition were used (same composition codes). The presence of a plant species refers to its presence in the seed mixture at plot establishment in 2002, independent of its actual abundance through 2006. Only the first four plant species hosted aphids in our study. *Ant*: *Anthriscus sylvestris*, *Arr*: *Arrhenatherum elatius*, *Phl*: *Phleum pratense*, *Tri p*: *Trifolium pratense*, *Alo*: *Alopecurus pratensis*, *Dac*: *Dactylis glomerata*, *Ger*: *Geranium pratense*, *Poa*: *Poa trivialis*, *Tri r*: *Trifolium repens*.

Block	Plot	Composition code	Species richness	Legume presence	*Ant*	*Arr*	*Phl*	*Tri p*	*Alo*	*Dac*	*Ger*	*Poa*	*Tri r*	Host plant biomass
2	86	S01M21	1		1									499.8
4	62	S01M21	1		1									356.7
3	57	S01M22	1			1								384.7
4	48	S01M22	1			1								374.2
2	8	S01M44	1				1							326.95
3	11	S01M44	1				1							199.65
2	20	S01M60	1	1				1						505.25
4	24	S02M18	2			1			1					101.35
1	92	S02M19	2		1	1								314.9
1	9	S02M24	2		1						1			37.105
4	54	S02M25	2			1					1			234.25
2	63	S02M27	2				1		1					48.55
3	9	S02M28	2		1		1							476.15
2	19	S02M29	2			1	1							680.95
3	33	S02M31	2				1				1			137.2
1	12	S02M37	2				1					1		406.3
4	2	S02M38	2	1				1	1					23.4
3	1	S02M39	2	1	1			1						858.15
1	39	S02M40	2	1		1		1						631.45
4	32	S02M41	2	1				1		1				32.155
3	28	S02M42	2	1				1			1			116.3
2	82	S02M43	2	1			1	1						513.1
2	69	S02M44	2	1				1				1		165.6
2	18	S02M46	2	1	1								1	309.15
2	25	S02M47	2	1		1							1	394.35
4	19	S02M50	2	1			1						1	273.3
3	75	S03M05	3			1	1				1			399.6
4	56	S03M13	3	1	1			1			1			290.785
1	41	S03M15	3	1		1	1	1						743.25
4	50	S03M15	3	1		1	1	1						271.45
4	35	S03M16	3	1	1			1				1		556.95
2	46	S03M20	3	1	1						1		1	435.85
4	43	S03M21	3	1			1				1		1	359.3
1	17	S04M20	4		1	1	1					1		379
1	54	S04M23	4	1	1	1		1			1			432.45
2	67	S04M23	4	1	1	1		1			1			248.9
2	91	S04M26	4	1			1	1			1	1		409.85
4	78	S04M27	4	1	1	1					1		1	271.25
4	36	S04M29	4	1	1				1			1	1	33.4
3	19	S04M34	4	1	1		1	1					1	364.65
2	64	S06M03	6	1		1	1	1	1	1		1		267.2
1	3	S06M06	6	1	1	1	1		1			1	1	248.85
1	11	S06M07	6	1	1		1			1	1	1	1	32.58
4	64	S06M08	6	1	1	1		1	1		1		1	178.67
2	2	S09M01	9	1	1	1	1	1	1	1	1	1	1	134.695
3	91	S09M01	9	1	1	1	1	1	1	1	1	1	1	153.15
4	12	S09M01	9	1	1	1	1	1	1	1	1	1	1	142.55
Total			**47**	**30**	**22**	**21**	**22**	**21**	**10**	**6**	**17**	**12**	**14**	

Table 3: Analyses of variance for host plant biomass and host plant nitrogen concentration. "Plant species richness" and "Legume presence" were tested against "Plotcode", all other terms against "Residuals". Directions of significant main effects (with 1 df) are indicated by arrows. P-values < 0.05 are printed in bold. df = degrees of freedom, MS = mean square.

	Host plant biomass					**Host plant nitrogen concentration**				
	df	**MS**	**F**	**P**		**df**	**MS**	**F**	**P**	
Plant species richness	1	706360	17.3	**0.0001**	↓	1	2.213	4.1	**0.0482**	↑
Legume presence	1	3422	0.1	0.7735		1	16.232	30.3	**<0.0001**	↑
Plotcode	44	40806	4.8	<0.0001		43	0.535	23.3	<0.0001	
Host plant species (non-legume vs. legume)	1	488148	57.0	**<0.0001**	↓	1	32.367	1407.3	**<0.0001**	↑
Host plant species (rest)	2	13823	1.6	0.2061		2	0.781	34.0	**<0.0001**	
Plant species richness x Host plant species (non-legume vs. legume)	1	261584	30.6	**<0.0001**		1	0.007	0.3	0.5832	
Plant species richness x Host plant species (rest)	2	50123	5.9	**0.0044**		2	0.007	0.3	0.7387	
Legume presence x Host plant species (rest)	2	19150	2.2	0.1142		1	0.028	1.2	0.2743	
Residuals	71	8558				60	0.023			

Table 4: Analyses of variance for the proportion of winged aphids. First analysis without covariables, second analysis with biomass and nitrogen concentration of aphid host plants as covariables. "Plant species richness" and "Legume presence" were tested against "Plotcode", all other terms against "Residuals". Directions of significant effects of the covariables are indicated by arrows. P-values < 0.05 are printed in bold. df = degrees of freedom, % SS = percent sum of squares explained.

	df	**%SS**	**F**	**P**	**df**	**%SS**	**F**	**P**	
Host plant biomass					1	9.4	14.6	**0.0006**	↑
Host plant nitrogen concentration					1	0.8	1.2	0.2812	
Plant species richness	1	4.7	4.5	**0.0406**	1	3.1	2.8	0.1001	
Legume presence	1	0.1	0.1	0.8004	1	0.1	0.0	0.8306	
Plotcode	42	44.5	1.6	0.0707	41	45.3	1.7	0.0602	
Aphid identity	9	18.4	3.0	**0.0066**	9	15.6	2.7	**0.0193**	
Plant species richness x Aphid identity	6	3.0	0.7	0.6147	6	4.7	1.2	0.3205	
Legume presence x Aphid identity	4	0.4	0.2	0.9598	3	1.2	0.6	0.6144	
Residuals	43	28.9			31	19.9			

Table 5: Analyses of variance for the proportion of emerged parasitoids. First analysis without covariables, second analysis with biomass and nitrogen concentration of aphid host plants as covariables. "Plant species richness" and "Legume presence" were tested against "Plotcode", all other terms against "Residuals". Directions of significant effects of the covariables are indicated by arrows. P-values < 0.05 are printed in bold. df = degrees of freedom, % SS = percent sum of squares explained.

	df	%SS	F	P	df	%SS	F	P	
Host plant biomass					1	11.6	40.7	**0.0078**	↑
Host plant nitrogen concentration					1	29.7	104.4	**0.0020**	↓
Plant species richness	1	11.6	11.8	**0.0016**	1	1.5	1.4	0.2481	
Legume presence	1	9.6	9.8	**0.0036**	1	0.3	0.3	0.5751	
Plotcode	34	33.6	0.4	0.9551	33	34.8	3.7	0.1535	
Aphid identity	3	23.4	3.5	0.0709	3	3.0	3.5	0.1640	
Plant species richness x Aphid identity	3	1.6	0.2	0.8689	3	12.5	14.6	**0.0270**	
Legume presence x Aphid identity	2	2.2	0.5	0.6345	1	5.8	20.3	**0.0204**	
Residuals	8	18.0			3	0.9			

Table 6: Analyses of variance for the proportion of female parasitoids. First analysis without covariables, second analysis with biomass and nitrogen concentration of aphid host plants as covariables. "Plant species richness" and "Legume presence" were tested against "Plotcode", all other terms against "Residuals". Directions of significant effects of the covariables are indicated by arrows. P-values < 0.05 are printed in bold. df = degrees of freedom, % SS = percent sum of squares explained.

	df	%SS	F	P	df	%SS	F	P	
Host plant biomass					1	4.1	6.2	**0.0251**	↓
Host plant nitrogen concentration					1	4.0	6.1	**0.0264**	↓
Plant richness	1	0.2	0.1	0.7068	1	0.3	0.3	0.6008	
Legume presence	1	10.6	9.5	**0.0043**	1	3.7	3.5	0.0704	
Plotcode	30	33.3	1.4	0.2182	29	30.3	1.6	0.1729	
Parasitoid identity	12	17.5	1.8	0.1069	11	22.1	3.1	**0.0234**	
Plant species richness x Parasitoid identity	10	14.4	1.8	0.1201	8	18.6	3.5	**0.0169**	
Legume presence x Parasitoid identity	7	3.6	0.6	0.7236	5	7.2	2.2	0.1109	
Residuals	25	20.4			15	9.9			

Table 7: Analyses of variance for the body weight of two primary parasitoid species (*Adialytus arvicola* and *Trioxys brevicornis*). Both parasitoid species developed only in aphids on non-legume host plant species. First analysis without covariables, second analysis with biomass and nitrogen concentration of aphid host plants as covariables. Covariables and "Sex" (incl. "Parasitoid identity x Sex" interaction) were tested against "Residuals", all other terms against "Plotcode". "Parasitoid identity" was tested at the "Plotcode" level in this analysis because in almost all cases only one of the two species was present in a plot. Directions of significant effects of the covariables are indicated by arrows. P-values < 0.05 are printed in bold. df = degrees of freedom, % SS = percent sum of squares explained.

	df	**%SS**	**F**	**P**	**df**	**%SS**	**F**	**P**	
Host plant biomass					1	6.1	67.1	**<0.0001**	↑
Host plant nitrogen concentration					1	2.5	27.4	**<0.0001**	↑
Plant species richness	1	0.3	1.4	0.2452	1	0.8	2.7	0.1228	
Legume presence	1	7.7	34.6	**<0.0001**	1	0.6	2.2	0.1584	
Parasitoid identity	1	1.7	7.7	**0.0103**	1	1.1	3.9	0.0664	
Plant species richness x Parasitoid identity	1	0.2	0.7	0.4190	1	0.1	0.5	0.5017	
Legume presence x Parasitoid identity	1	0.0	0.1	0.7088	1	0.2	0.8	0.3812	
Plotcode	24	5.3	2.6	0.0001	16	4.7	3.2	<0.0001	
Sex	1	2.8	32.8	**<0.0001**	1	2.4	26.3	**<0.0001**	
Parasitoid identity x Sex	1	0.7	8.2	**0.0043**	1	0.5	5.5	**0.0198**	
Residuals	938	81.3			879	80.9			

GENERAL DISCUSSION

"*The different histories and trajectories of aquatic and terrestrial ecology suggest either that different processes are at work in these systems, or that social and disciplinary forces constrain the thinking of scientists and lead to divergent lines of inquiry.*"
(Shurin et al. 2006)

"*Nothing before had ever made me thoroughly realise, though I had read various scientific books, that science consists in grouping facts so that general laws or conclusions may be drawn from them.*"
(Charles Darwin)

"*Progress is measured not only by the accumulation of definitive answers from testing falsifiable theories, but also by the generation of inspiration, the elucidation of possible answers, and the illumination of new intriguing questions.*"
(Aarssen 1997)

The central theme of this thesis is plant diversity in grasslands. We studied how plant diversity is maintained, how it influences and is influenced by invasion and subsequent community re-assembly, and how it affects higher trophic levels. We found that Janzen-Connell feedback effects are powerful mechanisms maintaining plant coexistence and diversity (Chapter 1). We also showed that in the context of invasion, these feedbacks may regulate invader dominance and may underlie the increased invasion resistance of diverse communities (Chapters 2 and 3). We furthermore demonstrated that invaded communities re-assemble toward functionally diverse states, either on the basis of resource or pathogen niches (Chapter 3). Finally, we found that plant diversity has cascading bottom-up effects on multi-trophic aphid–parasitoid food webs, mainly via changes in the abundance, species richness and quality of aphid host plants (Chapters 4 and 5). Detailed discussions of results are provided at the end of each chapter. This general discussion constitutes an endeavour to link all findings, discuss them in their entirety, elaborate on their potential applications and suggest avenues for future research.

Biodiversity maintenance: pathogens as drivers of coexistence, invasion and assembly

Negative soil feedbacks have previously been identified in a few plant species in dunes, old fields and grasslands (van der Putten et al. 1993, Bever 1994, De Deyn et al. 2003) and have been hypothesised to be involved in the maintenance of species` coexistence (Bever et al. 1997, Olff et al. 2000). However, we linked these feedbacks to Janzen-Connell effects and showed that they are widespread in grasslands and strong enough to maintain coexistence between three plant functional groups differing in their fitness (Chapter1). Traditionally, Janzen-Connell effects refer to herbivore and predator effects in coral reefs and tropical forests (Janzen 1970, Connell 1971), but we argue that negative feedbacks of soil pathogens in grasslands work in essentially the same way: by reducing the competitive ability of conspecifics (or con-functional groups) in the vicinity. Admittedly, these effects may operate across much smaller spatial scales in grassland plants compared with trees; but not necessarily so, since clonal grassland plants can grow very large (e.g. Harberd 1963). Furthermore, trees could be expected to accumulate more pathogens and thus exhibit stronger feedbacks simply due to their longer life span. However, some grassland plants can grow very old; for example, clones of the sedge *Carex curvula* can be several thousand years old (Steinger et al. 1996). Besides, negative soil feedbacks have been shown to develop quickly (see for example the periods of experimental soil conditioning in the range of only a few months in Klironomos 2002, Engelkes et al. 2008). Despite the unease that both tropical ecologists and grassland

pedologists might feel, we therefore advocate a synthesis of Janzen-Connell research and negative soil feedbacks. A joining of forces is likely to reveal that these pathogen-driven density-dependent effects are both prevalent and influential in many ecosystems.

Resource niches have clearly been the foremost concept of species coexistence up to now. However, it has been suggested that "apparent competition" imposed by shared predators, also termed "competition for predator-free space", might be as important as competition for resources (Holt 1984, Chesson and Kuang 2008). Concluding from our results, we join Chesson and Kuang (2008) and " *echo the call by Holt (1984) a quarter of a century ago to treat predation and competition even-handedly*", adding pathogens to the predation-side of the call. Obviously, the link between pathogens and coexistence is not new (e.g. reviewed by Hudson and Greenman 1998). Nevertheless, the majority of plant coexistence studies continue to focus on resource niches (e.g. Harpole and Tilman 2007, Hautier et al. 2009). In particular in relatively uniform environments such as grasslands, these resource niches are difficult to imagine and extremely hard to detect (but see the two mentioned studies for successful examples). Top-down niches, i.e. niches created by pathogens or predators instead of resources, might offer a much larger number of niche axes, especially considering the enormous diversity of pathogens (Hudson et al. 2006).

Furthermore, not only plant species coexistence but also invasion and community assembly seem to be driven by pathogen-free niches rather than, or at least in addition to, resource niches (Chapters 2 and 3). On the other hand, the fact that many species were dispersal-limited at our field site (Chapter 3, see also Roscher et al. 2009) and that assisted dispersal increased the speed of community change, could be an indication of additional neutral mechanisms, i.e. stochastic processes unrelated to the species` biology. However, dispersal-limitation is not necessarily a neutral force (Clark 2009) but may vary between species, potentially affecting assembly in a highly non-neutral way (e.g. as part of a colonisation-competition trade-off). We did not analyse invasion and community assembly on the species level, but such an analysis might provide interesting insights in this respect.

Biodiversity effects: invasion resistance, productivity and multi-trophic food webs

We have so far discussed pathogen niches as coexistence mechanisms and as structuring forces behind invasion and community assembly. Additionally, they could be important as mediators of positive biodiversity–ecosystem functioning relationships. We showed (Chapters 2 and 3) that higher species richness and functional group richness increases invasion resistance, confirming previous results (e.g. Knops et al. 1999, Hector et al. 2001); and we

found evidence for pathogen niches mediating this increased ecosystem functioning. Primary productivity was similarly increased by species richness and functional group richness (Chapter 3, see also Hooper et al. 2005 for a review, and Marquard et al. in press for details of the biodiversity-productivity relationship in the Jena Experiment) and it would be exciting to investigate whether pathogens played a role here. It is conceivable that in highly diverse communities, all species benefit from a "pathogen dilution" and perform better than in monoculture. This pathogen-related difference in productivity may explain a large part of the positive complementarity effect which has so far been mainly associated with resource partitioning. The observation of declining monoculture productivity over time in some biodiversity experiments (e.g. van Ruijven and Berendse 2009, Marquard et al. in preparation), partially being responsible for an increasingly positive biodiversity effect, supports this hypothesis (but also a resource-based explanation since most biodiversity experiments do not receive fertiliser). This potentially pathogen-driven biodiversity effect has not been tested in grassland plant communities. However, a recent publication from a very different field demonstrated the benefit of snail species diversity not only for lowering disease transmission rates but also for increased snail reproductive output in an environment regulated by the human pathogen *Schistosoma mansoni*, for which snails are an intermediate host (Johnson et al. 2009). This example highlights the direct value that the protection of biodiversity may have for humans.

We continued from these effects of plant diversity at the plant level to investigating the effects of plant diversity on higher trophic levels (Chapters 4 and 5). Previous research has shown that plant quality can have cascading effects over four trophic levels (e.g. Harvey et al. 2003, Härri et al. 2008) and that incredibly complex bottom-up interactions chains exist: For example, root herbivores, soil nematodes or microbes may influence the searching efficiency, life-history variables and population sizes of parasitoids of aboveground herbivores three trophic levels away, sometimes not even linked by the same plant individuals (Bezemer et al. 2005, Soler et al. 2007a, Soler et al. 2007b). In contrast to these plant-quality cascades, we demonstrated profound plant-diversity cascades affecting densities and species richness of organisms up to the fourth and fifth level of aphid–parasitoid food webs; although these were partially mediated via changes in plant quality.

In this thesis, we focussed on bottom-up effects of plant diversity on insects and did not consider top-down effects of insects on plants. However, the top-down effects certainly exist and, to include a further level of complexity, potentially respond to bottom-up effects, resulting in a feedback on the plant community. For example, we found that in high plant

diversity, host plant biomass and aphid densities were low, resulting in low secondary parasitoid densities. This could have a relaxing effect on their prey, primary parasitoids, which in turn could lead to reduced aphid densities, thus relieving herbivore pressure on the plant level. This example nicely demonstrates that in a food web of four or five trophic levels, the simultaneous study of bottom-up and top-down effects of diversity loss would be a rather ambitious (but no less exciting) undertaking.

Nevertheless, by taking top-down effects into account we might have detected a coexistence-maintaining effect of aphids on plants in the long run, akin to the originally proposed herbivore effect of the Janzen-Connell hypothesis (Janzen 1970, Connell 1971). Finally, it has been suggested lately that multi-trophic webs are assembled and multi-trophic diversity is maintained according to the same rules as in plant communities (Bastolla et al. 2009). Possibly, our findings from the plant community assembly experiment (Chapter 3) could therefore contribute to the research on food web structure, highlighting the need for a broader linkage between separate fields (see "*General recommendations*" below).

Potential applications

Biodiversity is rapidly disappearing in many parts of the world. Can this thesis make a contribution to halt this decline or to alleviate the negative effects on ecosystems and their functioning? Or as Srivastava and Vellend (2005) appropriately ask: "*Biodiversity–ecosystem function research: Is it relevant to conservation?*".

In Chapters 2 and 3 for example, we demonstrated that increased diversity indeed provides increased resistance against invasion at the local scale. In conservation practice, it might therefore be useful to shift the emphasis from the protection of rare or spectacular species (such as for example orchids) to the promotion of species-rich native communities, at least in ecosystems prone to exotic invasions. This could include the seeding of native species (Funk et al. 2008), thereby speeding up the natural colonisation process if native species are dispersal-limited (see Chapter 3). Furthermore, we showed that negative feedbacks resulting from pathogen or resource niches strongly limit the invasion of species from those functional groups that are already present in the resident community (Chapters 1 and 3). Increasing functional diversity and the abundance of native species that are closely related to or in the same functional group with locally problematic invaders might assist restoration efforts (e.g. Pokorny et al. 2005). As we and others have shown, increased propagule pressure may increase the speed of invasion, both for native (Chapter 3) and exotic invaders (e.g. Kolar and Lodge 2001, Lockwood et al. 2005, Von Holle and Simberloff 2005). Thus, large populations

of exotic invaders, for example in people's gardens, should be targeted and eradicated. Generally, the findings of basic community ecology should be considered more often in the management of exotic species (see "*General recommendations*" below).

In agriculture, negative soil feedbacks have been a topic for hundreds of years. There, they are often termed "soil sickness" and refer to both, pathogens and negative chemical effects (autotoxicity or nutrient depletion), affecting crops repeatedly grown at the same site. These feedbacks continue to be a problem in many regions of the world (e.g. Alsaadawi 2006, Sampietro 2006). We demonstrated that the agriculturally acknowledged pathogen effects also exist in natural systems and may affect plant competition and invasion very strongly (Chapters 1-3). Reversing the argument, we conclude that spatial or temporal diversity in agricultural cropping will be favourable to control pathogens and subsequently increase yield. Historically, this knowledge had been implemented for example through crop rotation; but with pesticides readily available, this practice has been largely abandoned. In addition to reviving traditional methods such as crop rotation, it would certainly be advantageous in terms of disease control to maintain plant genetical diversity by conserving and using old varieties (i.e. maintaining agrobiodiversity, Hammer et al. 2003), and by growing different varieties or genotypes in mixtures (Zhu et al. 2000). Of course, mixtures of different crop species instead of varieties would be even more effective (intercropping, e.g. Li et al. 2007) because they share fewer pathogens, but these mixtures are more costly in their maintenance and harvest.

In summary, by increasing agricultural diversity via crop rotation, intercropping or botanically diverse field margins (e.g. Thomas and Marshall 1999), farmers could reduce pathogen attack (Zhu et al. 2000), increase resource partitioning between crops (Li et al. 2007), reduce weeds (Smith and Gross 2007) and enhance biocontrol (Lavandero et al. 2006). Chemical input could be reduced while maintaining high yields and additionally providing services in terms of conservation and landscape aesthetics (Junge et al. in press). How many of these idealistic principles are practical and how they could best be realised remains to be studied. Here, improved collaboration between ecologists and agronomists would be desirable (see "*General recommendations*" below).

One of Srivastava's and Vellend's (2005) suggestions in order to make biodiversity-ecosystem function research more relevant to conservation is its expansion to multiple trophic levels. This multi-trophic approach has also been campaigned for by others (Duffy 2003, Worm and Duffy 2003, Thébault and Loreau 2005, Thébault and Loreau 2006, Duffy et al. 2007, McCann 2007, Thébault et al. 2007, Lewis 2009); and we happily followed their

suggestion in this thesis. We showed in Chapters 4 and 5 that species loss at the basis of the food web can indeed have profound cascading effects on species richness, abundance and life-history traits several trophic levels above. More specifically, very low plant diversity was detrimental especially for the first two trophic levels above plants, while very high plant diversity resulted in insufficient host densities and caused species extinctions at the highest trophic levels. The aim in grassland conservation should therefore be the preservation of species-rich plant communities of sufficient size with a high degree of connectivity between habitats to maintain stable multi-trophic communities.

Specific suggestions for future research

As mentioned above, resource niches are still regarded as the most important plant coexistence mechanism and resource complementarity is largely held responsible for the positive biodiversity–ecosystem functioning relationship. We conclude from the prevailing pathogen feedbacks in our experiments (Chapters 1 and 3), that more studies should consider pathogens as drivers of coexistence, invasion and ecosystem functioning. We furthermore suggest that future experiments explicitly test the strength of resource vs. pathogen effects in different ecosystems. Because we assessed Janzen-Connell effects in a large number of plant species, we did not inquire exhaustively about the specific mechanisms, for example the types of pathogens responsible. This could be the focus of additional experiments. Furthermore, if pathogens turn out to be important niche dimensions in many ecosystems, it will be essential to gain more knowledge about their respective host specificity (Gilbert 2005, Augspurger and Wilkinson 2007).

The results we report in Chapter 2 show that the lack of a negative feedback does not benefit exotic invaders in terms of a higher probability or speed of community entry, contrary to what has been implied by several recent studies. We conclude from these findings that future empirical studies should assess the process of enemy release in exotic invasions with more rigour. They should distinguish more clearly between fitness differences and the lack of density-dependent stabilising mechanisms (i.e. negative feedbacks). Furthermore, consequences of both effects should be tested separately for different stages of the invasion and in realistic scenarios with competition from co-occurring native species.

With increasing numbers of exotic invaders naturalising in native communities, it may further become essential to shift the focus from studying the invasion process to assessing the consequences of invaders for native communities, for example regarding their ecosystem functioning (Chapter 3, see also e.g. Maron and Marler 2008). Furthermore, diversity

maintenance and diversity effects in purely exotic versus purely native communities (Wilsey et al. 2009) as well as in mixed communities should be studied to predict changes in ecosystems when exotic species are integrated into native assemblages.

The aphid–parasitoid food webs in our studies (Chapters 4 and 5) incorporated several aphid and parasitoid generations. However, they were restricted to one season even though year-to-year variation in species links might be substantial (Petanidou et al. 2008). In webs consisting of specialists such as aphid–parasitoid food webs, this temporal variation might not be as large as in more generalised networks. Still, it would be useful to extend our study to several years. The inclusion of aphid predators in the food webs, though much more difficult to achieve at least in quantified form (van Veen et al. 2008), would provide more insights, especially because predators are more generalised in their feeding habits than parasitoids. Therefore, interactions strengths which were highly correlated with species richness of the webs in our study due to the specialist nature of aphids and parasitoids could vary between communities of the same insect species richness. By examining the change in interaction strengths across plant species richness levels, additional "hidden" effects of plant diversity on food web structure might be picked up (Tylianakis et al. 2007). Finally, more realistic scenarios of species loss should be studied, especially in a multi-trophic context where extinctions are rarely balanced between trophic levels (Duffy 2003). As predators are often lost first from ecosystems, this would mean including top-down forces into future studies, as mentioned above.

General recommendations and conclusions

Our aphid-parasitoid work (Chapters 4 and 5) demonstrated that food webs can be valuable tools to assess effects of plant species loss. Therefore, we propose that research should proceed from complex analyses of status-quo food webs to making use of food webs as tools in the evaluation of environmental change. For example, food webs could be used more often to investigate consequences of habitat modification due to agriculture (Albrecht et al. 2007, Tylianakis et al. 2007, Macfadyen et al. 2009), effects of global change, especially in terms of climate change and CO_2 levels (Petchey et al. 1999, Emmerson et al. 2004, van der Putten et al. 2004, Emmerson et al. 2005), or impacts of invasive species (Schönrogge and Crawley 2000, Henneman and Memmott 2001).

The diversity of topics in this thesis, including biodiversity maintenance and biodiversity effects, belowground and aboveground processes, plants and animals, gave rise to the conclusion that progress in science is facilitated by linking previously separate fields and

by thinking across traditional borders. In this thesis, we started this process by applying a coexistence mechanism from tropical forests and coral reefs to temperate grasslands, by linking research on coexistence, community assembly and exotic invasions, and by studying food webs in a biodiversity context. Other recent "cross-border" examples include links between other community ecological concepts and exotic invasions (Davis et al. 2001, Shea and Chesson 2002, Cadotte et al. 2006, Funk et al. 2008), between community assembly and restoration (Temperton et al. 2004, Leps et al. 2007, Funk et al. 2008, Kardol et al. 2008), between evolution and ecosystem functioning (Harmon et al. 2009), between other measures of diversity such as evenness or phylogenetic distance and ecosystem functioning (Cadotte et al. 2008, Hillebrand et al. 2008), between mutualistic networks and coexistence (Bastolla et al. 2009), between pollination and plant community assembly (Sargent and Ackerly 2008), between infectious diseases and biodiversity effects (Johnson et al. 2009) and between agriculture and biodiversity–ecosystem functioning (Weiner 2003, Li et al. 2007, Smith and Gross 2007). The strengthening of links between different fields and the increased generalisation of concepts is expected to lead to the emergence of new ideas and new unifying - hopefully slightly less neutral - theories. Macfayden (1975) demands that "*ecology must remain a unified science*", however, it should as a first step achieve this unity.

The last century was perhaps the time to discover, describe, inventory and marvel about the countless species, their habits and habitats, and ecological research has generated plenty of knowledge and many now classical theories (Elton 1927, Hutchinson 1957, Elton 1958, Hairston et al. 1960, MacArthur and Wilson 1963, Paine 1966, MacArthur and Levins 1967, MacArthur and Wilson 1967, Janzen 1970, Petermann 1970, Connell 1971, May 1972, Root 1973, Diamond 1975, Paine 1980, Abrams 1983, Holt 1984). Discoveries are still being made, be it a few newly evolved tree species such as the No parking Whitebeam (*Sorbus admonitor*) in Great Britain earlier this year (Rich and Proctor 2009), vegetarianism in a jumping spider (Meehan et al. 2008) or an undescribed wasp species in this thesis (Chapter 4).

However, the era of big ecological discoveries is probably over and we better move on. Only during the four years of work on this thesis, the CO_2 content of the atmosphere has increased by 7.6 ppm, the temperature has risen by 0.052 °C (IPCC 2007), 62 million hectares of forest have been destroyed (UNEP 2001) and about 100,000 species have been lost (estimation from the UN Convention on Biological Diversity, cited in Warren 2008). While traditional methods such as taxonomy should not be disregarded (Wilson 1985, Gotelli 2004, Godfray 2007) and classical theories should be revisited, we have to focus on applying our

knowledge and using the available tools to predict, prevent and alleviate the consequences of environmental change for ecosystems.

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SUMMARY

"*And NUH is the letter I use to spell Nutches*
Who live in small caves, known as Niches, for hutches,
These Nutches have troubles, the biggest of which is
the fact there are many more Nutches than Niches.
Each Nutch in a Nich knows that some other Nutch
Would like to move into his Nich very much.
So each Nutch in a Nich has to watch that small Nich
Or Nutches who haven't got Niches will snitch."
(Dr. Seuss, 1955)

In a rapidly changing world suffering from extensive diversity loss, the most pressing questions remain largely unanswered: how can diversity exist in the first place and what are the consequences of its decline for ecosystems? In grasslands, resource niches have to date been considered the major mechanism responsible for plant coexistence and diversity. The neutral theory has recently challenged this view by attributing species coexistence solely to stochastic processes. Whereas the negative effects of plant diversity loss on primary productivity have been demonstrated numerous times in biodiversity experiments, its effects on higher trophic levels have rarely been explored. Here, we used a glasshouse experiment, simulation modelling approaches and field studies in the Jena biodiversity experiment to examine diversity maintenance, invasion and community assembly in plant communities and effects of plant diversity loss on higher trophic levels.

In **chapter 1** we report results from an experiment that studied Janzen-Connell effects as drivers of grassland plant coexistence and diversity. We used soil trained by field monocultures and measured the negative feedbacks on plants growing on soil from their own species compared with other soils in the glasshouse. We found that especially in competition with other plant functional groups nearly all species suffered from strong negative soil feedbacks that were most likely caused by non-fungal soil pathogens. With a simulation model, we showed that these pathogen feedbacks were strong enough to maintain coexistence between three plant functional groups.

In **chapter 2** we continued to explore these feedbacks but in the context of exotic invasions. We used an analytical and a simulation modelling approach to show that the lack of negative feedbacks does not enhance the probability or the speed at which exotic plants invade native communities. We found that higher invader fitness is much more important in this context. Furthermore, we demonstrated that community regulation by negative feedbacks might be responsible for the higher invasion resistance of diverse communities.

In **chapter 3** we studied mechanisms of invasion and community assembly in the Jena Experiment by following the development of established communities of different original diversity after opening them to invasion. We examined conditions of both natural invader dispersal and dispersal assisted by seed addition and found that invasion was strongly controlled by the negative effects of residents on invader species of the same functional group, with only a limited importance of chance effects of dispersal. Furthermore, communities re-assembled toward high-diversity states but not always with maximum productivity, indicating a role for pathogens in addition to resources.

In **chapter 4** we used plant communities of the Jena Experiment to examine effects of plant diversity on aphid–parasitoid food webs in the field. We measured the density and species richness of aphids, primary and secondary parasitoids in plant communities varying in species richness and applied structural equation models to tease apart direct and indirect effects. We found that plant species richness had an impact on species at all levels of the food web and that the effects operated predominantly indirectly via lower trophic levels. Intermediate plant species richness proved to be most favourable for aphids and primary parasitoids. The higher the trophic level of the organisms, the earlier negative effects of plant species richness set in as a result of low host abundance.

In **chapter 5** we investigated the effects of plant diversity on life-history traits of aphids and their parasitoids again using the plots of the Jena Experiment. We showed that plant species richness had a negative effect on the proportion of winged aphids, potentially as a result of strong resource limitation, and a negative effect on parasitoid emergence rates and proportions of females, potentially as a result of increased aphid defences in high-nitrogen environments. In contrast, legume presence and associated high nitrogen concentrations in the plant community increased the body weight of the two most abundant primary parasitoids.

We conclude from our results that grassland plant diversity is more often maintained by pathogen niches (Janzen-Connell effects) than previously thought. Furthermore, pathogens in addition to resources play a role in plant invasion and make community assembly biologically predictable rather than neutral. We further demonstrate that plant diversity does not only increase plant community invasion resistance but also influences aphid–parasitoid food webs up to the fourth an fifth trophic level, advocating a multi-trophic view in biodiversity research and conservation. We emphasise that linking previously separate lines of research will help to advance the field of ecology and enable us to meet the challenges posed by environmental change.

ZUSAMMENFASSUNG

"*Schläft ein Lied in allen Dingen,*
Die da träumen fort und fort.
Und die Welt hebt an zu singen,
Triffst du nur das Zauberwort."
(Joseph von Eichendorff)

"*Je mehr ich Pflanzen beobachte, desto mehr wachsen sie in meiner Achtung.*"
(Charles Darwin)

Unsere Welt ist einem schnellen Wandel unterworfen und während weiterhin Tier- und Pflanzenarten aussterben, sind wesentliche Aspekte der Artenvielfalt noch weitgehend unverstanden: warum existiert überhaupt so viel Vielfalt und was sind die Konsequenzen für unsere Ökosysteme wenn wir diese Vielfalt Stück für Stück verlieren? In Wiesenökosystemen wurde bis jetzt davon ausgegangen, dass die Koexistenz der Pflanzenarten sich vor allem durch Ressourcennischen erklären lässt. Erst die neutrale Theorie hat diese Erklärung ernsthaft in Frage gestellt, indem sie die Koexistenz von Arten ausschliesslich zufälligen Prozessen zuschrieb. In zahlreichen Biodiversitätsexperimenten wurde bereits gezeigt, dass der Verlust von Pflanzenarten einen negativen Einfluss auf die Primärproduktivität hat. Wie sich hingegen der Rückgang der Pflanzenvielfalt auf höhere trophische Ebenen auswirkt, wurde bis jetzt kaum erforscht. Für die vorliegende Arbeit wurden ein Gewächshausexperiment, sowie Freilandarbeiten im Jena Biodiversitätsexperiment durchgeführt und Simulationsmodelle angewendet. Mit diesen Untersuchungen sollte geklärt werden, wie die Koexistenz in Pflanzengemeinschaften aufrechterhalten wird, welche Mechanismen die Invasion neuer Arten und die Gemeinschaftsbildung (community assembly) steuern und wie die Pflanzenvielfalt höhere trophische Ebenen beeinflusst.

In **Kapitel 1** untersuchten wir Janzen-Connell Effekte als Mechanismen der Pflanzenkoexistenz und -vielfalt in Wiesengemeinschaften. In einem Gewächshausversuch mit Boden von Freiland-Monokulturen wurden die negativen Rückkopplungen (negative feedbacks) der Pflanzenarten bei Anzucht auf ihrem eigenen Boden im Verhältnis zu artfremden Böden ermittelt. Wir stellten fest, dass, vor allem in Konkurrenz mit anderen funktionellen Gruppen, fast alle Arten starke negative Rückkopplungen zeigten, die wahrscheinlich auf nicht-pilzliche Pathogene zurückzuführen waren. Mit Hilfe eines Simulationsmodells wiesen wir nach, dass diese Pathogeneffekte stark genug waren, um die Koexistenz dreier funktioneller Gruppen aufrecht zu erhalten.

Auch in **Kapitel 2** beschäftigten wir uns mit diesen Rückkopplungen, allerdings im Zusammenhang mit der Einwanderung exotischer Arten. Wir benutzten einen analytischen Lösungsweg sowie ein Simulationsmodell um zu zeigen dass das Fehlen negativer Rückkopplungen in nicht-einheimischen Pflanzenarten weder die Wahrscheinlichkeit noch die Geschwindigkeit einer Einwanderung erhöht. Die höhere Fitness der einwandernden Arten ist hier offensichtlich wichtiger. Des Weiteren konnten wir zeigen, dass bei diversen Pflanzengesellschaften solche Rückkopplungen für deren höhere Invasionsresistenz verantwortlich sein können.

In **Kapitel 3** untersuchten wir der Invasion und der Gemeinschaftsbildung zugrunde liegende Mechanismen innerhalb des Jena Experiments. Dazu öffneten wir Pflanzengemeinschaften verschiedener ursprünglicher Diversität der Einwanderung neuer Arten, entweder unter natürlichen Verbreitungsbedingungen oder mit Hilfe von Samenzugabe. Wir stellten fest, dass die Invasion stark von negativen Effekten der etablierten Arten auf einwandernde Arten der gleichen funktionellen Gruppe kontrolliert wurde. Zufallseffekte der Verbreitung waren hingegen weniger wichtig. Die Gemeinschaften reorganisierten sich während und nach der Invasion in Richtung hoch-diverser Systeme, aber nicht immer mit der höchsten Produktivität. Dies deutet an, dass für solche Prozesse Pathogene - neben Resourcen - ebenfalls eine wichtige Rolle spielen.

In **Kapitel 4** nutzten wir das Jena Experiment, um Auswirkungen der Pflanzenvielfalt auf Blattlaus-Parasitoiden-Nahrungsnetze im Freiland zu untersuchen. Wir ermittelten die Dichte und Artenzahl von Blattläusen, Primärparasitoiden und Sekundärparasitoiden und wendeten Strukturgleichungsmodelle an, um direkte und indirekte Effekte zu trennen. Die Pflanzenvielfalt hatte einen Einfluss auf das gesamte Nahrungsnetz, jedoch waren die Effekte grösstenteils indirekt und wurden über die unteren trophischen Ebenen übertragen. Mittlere Pflanzenvielfalt erwies sich als vorteilhaft für Blattläuse und Primärparasitoide. Je höher die trophische Stufe der Organismen, desto eher setzten negative Effekte der Pflanzenvielfalt ein, die von der niedrigen Wirtshäufigkeit herrührten.

In **Kapitel 5** untersuchten wir die Effekte der Pflanzenvielfalt auf demographische Merkmale von Blattläusen und ihren Parasitoiden, erneut unter Verwendung der Versuchsflächen im Jena Experiment. Die Pflanzenvielfalt hatte einen negativen Einfluss auf den Anteil geflügelter Blattläuse, was möglicherweise auf eine starke Ressourcenlimitierung zurückzuführen ist. Auch konnte ein negativer Effekt der Pflanzenvielfalt auf den Anteil geschlüpfter Parasitoide sowie weiblicher Parasitoide beobachtet werden. Dieser Effekt ist vermutlich bedingt durch eine verstärkte physiologische Abwehr der Blattläuse in Gemeinschaften mit erhöhten Stickstoffkonzentrationen. Im Gegensatz dazu erhöhte die Anwesenheit von Leguminosen und die damit höhere Stickstoffkonzentration in der Pflanzengemeinschaft das Körpergewicht der zwei häufigsten Primärparasitoidenarten.

Wir schliessen aus unseren Ergebnissen, dass die Pflanzenvielfalt in Wiesenökosystemen öfter als bisher vermutet durch Pathogennischen (Janzen-Connell Effekte) aufrechterhalten wird. Des Weiteren spielen Pathogene zusätzlich zu Ressourcen bei der Einwanderung eine Rolle und machen die Gemeinschaftsbildung von Pflanzen eher biologisch vorhersagbar als neutral. Die Pflanzenvielfalt erhöht zudem nicht nur die

Invasionsresistenz der Pflanzengemeinschaft sondern beeinflusst auch Blattlaus-Parasitoiden-Nahrungsnetze bis zur vierten und fünften trophischen Stufe. Vor diesem Hintergrund empfiehlt sich in der Biodiversitätsforschung und im Naturschutz eine multi-trophische Sichtweise. Zudem könnte eine bessere Vernetzung bislang getrennter ökologischer Forschungsgebiete einen wichtigen Schritt darstellen, um die Herausforderungen des globalen Wandels zu meistern.

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CURRICULUM VITAE

"*Pessimism of the mind, optimism of the spirit.*" (Antonio Gramsci)
(from Hoare and Nowell-Smith 1971, cited in Weiner 1999)

"*Botanists are more civilized than zoologists.*"
(Goose biologist, cited by Peter Kotanen on www.erin.utoronto.ca/~w3pkota)

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